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Collybiopsis and its type species, *Co. ramealis*

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Abstract—*Collybiopsis* (*Omphalotaceae*, *Agaricales*) is accepted as the correct genus name for a large clade of non-typical *Gymnopus*. The type species of *Collybiopsis* (*Agaricus ramealis*) is shown to be a genetic complex. *Collybiopsis filamentipes*, *Co. furtiva*, *Co. hasanskyensis*, and *Co. minor* are proposed as spp. nov. and *Co. californica* as a stat. nov. Thirty-four additional *Collybiopsis* comb. nov. are proposed in Appendix I.

Key words—clade /marasmiellus, morphology, taxonomy, new combinations, new species

Introduction

For many years, agaric taxonomists have dealt with the morphological and molecular diversity of both *Gymnopus* and *Marasmius*. Several segregate genera have been carved from *Gymnopus*, but a large complex of fungi remains, comprising taxa contributed by elements of *Gymnopus*, *Marasmius*, and *Marasmiellus*. This large assemblage has been called *Marasmiellus* (see Wilson & Desjardin 2005), presumably because the type species of *Marasmiellus*, *Ma. juniperinus*, is included. Recent papers by Dutta & al. (2015) and Oliveira & al. (2019) are among the latest to draw attention to *Marasmiellus*. Two principles were included: 1) presentation of a well-populated phylogeny to demonstrate placement of numerous taxa exhibiting "gymnopoid," "marasmioid," and/or "marasmielloid" taxonomic character suites; and 2) the use of the genus name *Marasmiellus* to represent a large taxonomic group that includes type species of at least two genera (*Marasmiellus* and *Collybiopsis*) plus taxa of *Gymnopus* sect. *Vestipedes*. While we agree with the taxonomy presented, we choose to follow the International Code of Nomenclature (Turland & al. 2018, Art. 11.3) in accepting the prior genus name, *Collybiopsis*, for the group that Oliveira & al. (2019) and Wilson & Desjardin (2005) called *Marasmiellus*.

Nomenclaturally, *Collybiopsis* Earle 1909 (with its explicit type species *Agaricus ramealis* Bull. 1787) has clear priority over *Marasmiellus* Murrill 1915 (explicitly typified by *Ma. juniperinus* Murrill). Use of *Marasmiellus* for this clade would require conservation of this genus name, not yet proposed. In addition, *Ma. juniperinus* is poorly represented phylogenetically (two ITS-based sequences, neither from the topotype location). Conversely, *Co. ramealis* is a well-known taxon molecularly represented from original topotype locales. The relative placement of these taxa is shown in Figs 1, 2. To our knowledge, only Horak (1971) has recombined basionyms into *Collybiopsis*.

Taxonomic circumscription of fungi assigned to *Marasmiellus*-like taxa has changed and enlarged over the last century. Although an extensive literature chronology could be narrated, this is not the intent of this paper. Instead, literature can be concisely cited, leaving further investigation to the reader. A sketch of this morpho-taxonomic process includes: Antonín & Noordeloos (1993, 1997, 2010); Clements & Shear (1931, 1954); Corner (1996); Donk (1962); Earle (1909); Horak (1968); Kühner (1933, 1936); Murrill (1915); Patouillard (1900); Singer [1936, 1945, 1948, 1962—dismissing *Collybiopsis* and accepting *Marasmiellus* with 59 species; for more on this, see "Discussion"—and 1973 with 134 species listed in *Marasmiellus*]. Since the introduction of molecular tools in fungal taxonomy, numerous papers have presented phylogenetic trees including or alluding to the group under consideration. These papers include Aldrovandi & al. (2015); Binder & Hibbett (2002); Dentinger & al. (2016); Desjardin (1997); Desjardin & al. (2017); Desjardin & Perry (2017); Dutta & al. (2015); Honan & al. (2015); Hughes & Petersen (2015); Hughes & al. (2001, 2008); Kerekes & Desjardin (2009); Kim & al. (2015); Mata & al. (2004, 2007); Matheny & al. (2006); Moncalvo & al. (2000, 2002); Nakasone & al. (2009); Oliveira & al. (2019); Petersen & Hughes (2014, 2016, 2017a,b); Sandoval-Leiva & al. (2016); and Wilson & Desjardin (2005).

The intent of this paper is to endorse use of *Collybiopsis* over *Marasmiellus*, especially by (re)describing taxa within the *Co. ramealis* complex with emphasis on European collections of *Co. ramealis*. A list of proposed transfers into *Collybiopsis* appears in Appendix I.

Table 1. Collections used in phylogenetic analyses. (HT = holotype; ET = epitype)

Organism	Herbarium No.	Isolate	Location	Fig. no.	GenBank ITS	GenBank LSU
Collybiopsis biformis						
Co. biformis	TENN-F-068109	TFB14251	USA: Tennessee, GSMNP	1	KJ416245	KJ189567
Co. biformis	TENN-F-68108	TFB14250	USA: Tennessee, GSMNP	1	KJ416246	KJ189568
Co. biformis	TENN-F-065586	TFB13890	USA: North Carolina	1	KJ416248	KJ189570
Co. biformis	TENN-F-065189	TFB13814	USA: Tennessee	1	KJ416249	KJ189569
Collybiopsis brunneigracilis						
Co. brunneigracilis	AWW01-SFSU	AWW01	Java/Bali	1	AY263434	AY639412
Collybiopsis californica						
Co. californica	Environmental	—	USA: California	1, 2	DQ273359	—
Co. californica	Environmental	—	USA: Oregon	1, 2	HM488468	—
Co. californica	Environmental	—	USA: Oregon	1, 2	HM488469	—
Co. californica	SFSU: Wright866	Wright866	USA: California	1, 2	MN413335	—
Co. californica	SFSU-F-024539	Wright2941	USA: California	1, 2	MN413336	—
Co. californica	SFSU-F-024526	DED8372	USA: California	1, 2	MN413337	—
Co. californica	TENN-F-052617	TFB5787	Canada: British Columbia	1, 2	MN413338	—
Collybiopsis confluens* ssp. *americana						
Co. confluens ssp. *americana* [HT]	TENN-F-069073	TFB14409	Canada: New Brunswick	1	KP710278	KJ189585
Co. confluens ssp *americana*	TENN-F-069053	TFB14389	Canada: New Brunswick	1	KP710279	KJ189584
Co. confluens ssp *americana*	TENN-F-067822	TFB14075	USA: North Carolina	1	KP710281	KJ189581
Collybiopsis confluens						
Co. confluens	TENN-F-067865	TFB14115	Germany, Thuringia	1	KP710292	KJ189578
Co. confluens	TENN-F-067864	TFB14114	Germany, Thuringia	1	KP710296	KJ189573
Collybiopsis dichroa						
Co. dichroa	TENN-F-056721	TFB10009	USA: North Carolina	1	KY026654	KY026654
Co. dichroa	TENN-F-067859	TFB14111ss1	USA: Tennessee, GSMNP	1	KY026696	KY026696
Co. dichroa	TENN-F-067859	TFB14111ss2	USA: Tennessee, GSMNP	1	KY026697	KY026697
Co. dichroa	TENN-F-056584h1	TFB9623	USA: North Carolina	1	MW396865	MW396865
Co. dichroa	TENN-F-056584h2	TFB9623	USA: North Carolina	1	MW396866	MW396866

Organism	Herbarium No.	Isolate	Location	Fig. no.	GenBank ITS	GenBank LSU
Co. dichroa	TENN-F-065569	TFB13873	USA: North Carolina	1	MW396867	MW396867
Co. dichroa	TENN-F-051775	TFB5459	USA: South Carolina	1	MW396868	MW396868
Co. dichroa	TENN-F-048680	TFB1860	USA: North Carolina	1	MW396869	MW396869
Collybiopsis disjuncta						
Co. disjuncta	TENN-F-068136	TFB14281	USA: Mississippi	1	KJ416253	KY019643
Co. disjuncta [HT]	TENN-F-069172	TFB14339	USA: Connecticut	1	NR_137865	—
Collybiopsis eneficola						
Co. eneficola	TENN-F-069122	10-09-021AV04	Canada: Newfoundland	1	KJ128265	KJ189590
Co. enificola	MICH:PK6975	PK6975	Alaska	1	KP710270	KP710304
Co. enificola	MICH:PK6975	PK6976	Alaska	1	KP710271	KP710305
Co. eneficola [HT]	TENN-F-069123	09-09-26AV13	Canada: Newfoundland	1	NR_137613	NG_059502
Collybiopsis filamentipes						
Co. filamentipes	environmental	KTRF390	Canada: Alberta	1	MG433317	
Co. filamentipes	TENN-F-065861	TFB13962	USA: Tennessee	1	MN897832	MN897832
Collybiopsis foliiphila						
Co. foliiphila	CUM AM101	—	India	1	KP317638	KP317636
Co. foliiphila [HT]	CUH AM090	—	India	1	NR_154176	NG_060320
Collybiopsis furtiva						
Co. furtiva as M. ramealis	SFSU: DED4425	DED4425	USA: North Carolina	2	DQ450031	AF042650
Co. furtiva	SFSU-F-024523	DED3973	USA: North Carolina,	1, 2	MN413339	—
Co. furtiva	SFSU-F-024508	DED4584	USA: North Carolina	1, 2	MN413340	—
Co. furtiva	SFSU-F-024524h1	DED5796h1	USA: North Carolina	1, 2	MN413341	—
Co. furtiva	SFSU-F-024524h2	DED5796h2	USA: North Carolina	1, 2	MN413342	—
Co. furtiva (as Marasmiellus)	TENN-F-051097	TFB4796	USA: Georgia	1, 2	MN413343	MW396879
Collybiopsis gibbosa						
Co. gibbosa	MEL:2382838	—	Australia	1	KP012713	KP012713
Co. gibbosa	URM 90012	—	Brazil	1	KY061202	KY061202
Co. gibbosa	URM 90006	—	Brazil	1	KY061203	KY061203
Collybiopsis hasanskyensis						
Co. hasanskyensis	TENN-F-060730	TFB11846	Russia: Kedrovaya	1	MN897829	—
Co. hasanskyensis	TENN-F-060731	TFB11847	Russia: Kedrovaya	1	MN897830	—

Organism	Herbarium No.	Isolate	Location	Fig. no.	GenBank ITS	GenBank LSU
Collybiopsis juniperina						
Co. juniperina	TENN-F-059540	TFB9889	USA: Louisiana	1	AY256708	KY019637
Co. juniperina	TENN-F-058988	TFB10782	Argentina: Missiones	1	KY026661	KY026661
Collybiopsis luxurians						
Co. luxurians	TENN-F-057910	TFB10350	USA: North Carolina	1	AY256709	AY256709
Co. luxurians	TENN-F-050619	TFB4283ss10	Sweden	1	KJ416240	—
Co. luxurians	TENN-F-055748	TFB9121	USA: Louisiana	1	KY026649	KY026649
Co. luxurians	TENN-F-067806	TFB14060	USA: North Carolina	1	MW396871	MW396871
Collybiopsis melanopus						
Co. melanopus	CUH AM093	—	India	1	KM896875	KP100305
Co. melanopus [HT]	SFSU: AWW54	AWW54	Java/Bali	1	NR-137539	NG_060624
Collybiopsis menehune						
Co. menehune [HT]	SFSU: DED5866 Holotype	—	Hawaii	1	AY263426	—
Co. menehune	SFSU-AWW15	—	Java/Bali	1	AY263443	AY639424
Co. menehune	Culture only	TFB11587, D. E. Hemmes 2320	Hawaii	1	DQ450043	—
Co. menehune	CUH AM089	—	India	1	KJ778753	KP100306
Collybiopsis mesoamericana						
Co. mesoamericana	NYBG:REH7379	REH7379	Costa Rica	1	AF505768	—
Co. mesoamericana	TENN-F-058106	TFB10411	Costa Rica	1	DQ450036	—
Co. mesoamericana [HT]	TENN-F-058613 Type	TFB11005	Costa Rica	1	NR_119583 = DQ450035	KY019632
Collybiopsis minor						
Co. minor	TENN-F-059993	TFB11930	USA: Tennessee, GSMNP	1, 2	MN413334	MW396880
Co. minor	TENN-F-051792	TFB5434	USA: South Carolina	1, 2	MW396872	MW396872
Co. minor	TENN-F-052933	TFB6284	USA: South Carolina	1, 2	MW405778	—
Collybiopsis neotropica						
Co. neotropica	TENN-F-058110	TFB10416	Costa Rica	1	AF505769	—
Collybiopsis nonnulla						
Co. aff *nonula*	TENN-F-068085	TFB14492	USA: Mississippi	1	KY026699	KY026699

ORGANISM	HERBARIUM NO.	ISOLATE	LOCATION	FIG. NO.	GENBANK ITS	GENBANK LSU
Co. aff *nonula*	TENN-F-068133	TFB14278	USA: Mississippi	1	KY026701	KY026701
Collybiopsis nonnulla var attenuatus						
Co. nonnulla v *attenuata*	SFSU: AWW05	AWW05	Java/Bali	1	AY263445	AY639426
Co. nonnulla v *attenuata*	SFSU: AWW55	AWW55	Java/Bali	1	AY263446	—
Co. nonnulla v *attenuata*	—	RAK369.2	Cameroon	1	MN930621	—
Co. nonnulla v *attenuata*	—	RAK372.2	Cameroon	1	MN930622	—
Co. obscuroides						
Co. obscuroides	GB-0150514	—	Norway: Svalbard	1	KX958399	KX958399
Co. obscuroides	GB-005381	—	Sweden: Jamtland	1	KX958498	KX958498
Collybiopsis parvula						
Co. parvula	TENN-F-058116	TFB10422	Costa Rica	1	AF505774	—
Co. parvula	TENN-F-058115	TFB10421	Costa Rica	1	DQ450061	—
Co. parvula	TENN-F-058119	TFB10425	Costa Rica	1	DQ450062	—
Co. parvula as *Marasmiellus parvulus*	—	SR83-10MX	Mexico	1	KT697977	—
Co. parvula as *G.* sp. VC-2017k	URM 90054		Brazil	1	KY404984	
Co. parvula [HT]	TENN-F-058113	TFB10419	Costa Rica	1	NR_119584.1 = DQ450060	—
Collybiopsis peronata						
Co. peronata	UBCF28402		Canada: British Columbia	1	KP454027	—
Co. peronata	TENN-F-065120	TFB13743	Belgium	1	KY026677	KY026677
Co. peronata	Culture only	LE-Bin1364	Russia	1	KY026755	KY026755
Co. peronata as *Gymnopus peronatus*	CBS 223.37	—	unknown	1	MH855896	MH867405
Collybiopsis polygramma						
Co. polygramma	TENN-F-056589	PR2542TN	Puerto Rico	1	AY842954	—
Co. polygramma	TENN-F-056589	TFB9628	Puerto Rico	1	DQ450028	—
Co. polygramma	—	SFC20120821-64	Korea	1	KJ609162	—
Co. polygramma	CUH:AM082	—	India	1	KJ778752	KP100303
Co. polygramma	URM 90015	—	Brazil: Amapa	1	KY074640	KY088275
Co. polygramma	URM 90016	—	Brazil: Amapa	1	KY074641	KY088274

Organism	Herbarium No.	Isolate	Location	Fig. no.	GenBank ITS	GenBank LSU
Co. polygramma	URM 90017	—	Brazil: Para	1	KY074642	—
Co. polygramma	MHHNU 30912	—	China	1	MK214392	—
Co. polygramma	HFJAU 0425	—	China: Jiangxi	1	MN258643	—
"Collybiopsis pseudoluxurians"						
Co. pseudoluxurians [HT]	TENN-F-068144	TFB14290	USA: Mississippi	1	KY026702; NR_137863	KJ416242
"Collybiopsis pseudomphalodes"						
"Co. pseudomphalodes"	NYBG REH7348	REH7348	Costa Rica	1	AF505762	—
"Co pseudomphalodes"	not given	PR24TN	Puerto Rico	1	AY842957	—
Collybiopsis quercophila						
Co. quercophila	TENN-F-069267	TFB14570	Slovakia	1	KY026728	KY026728
Co. quercophila	TENN-F-069320	TFB14615	USA: California	1	KY026736	KY026736
Co. quercophila	TENN-F-069321	TFB14616	USA: California	1	KY026737	KY026737
Co. quercophila	SFSU:25220	—	USA: California	1	KY026761	KY026761
Collybiopsis ramealis						
Co. ramealis	TENN-F-050324	TFB4727	Sweden	2	DQ450030	—
Co. ramealis	TENN-F-062867	TFB13520	Sweden	2	JF313670	—
Co. ramealis	TENN-F-065132	TFB13755	Belgium: Couvin	2	KJ416235	KJ189566
Co. ramealis	TENN-F-067890	TFB14140c1	Germany	2	KJ416235	KJ189566
Co. ramealis	TENN-F-065136	TFB13759	Belgium: Couvin	2	MN413344	—
Co. ramealis [ET]	TENN-F-065145	TFB13769	Belgium: Couvin	2	MN413345	MN413345
Co. ramealis	TENN-F-065146	TFB13770	Belgium: Couvin	1, 2	MN413346	MW396882
Co. ramealis	TENN-F-065147	TFB13771h1	Belgium: Couvin	2	MN413347	—
Co. ramealis	TENN-F-065147	TFB13771h2	Belgium: Couvin	2	MN413348	—
Co. ramealis	TENN-F-065151	TFB13775	Belgium: Dinante	2	MN413349	—
Co. ramealis	TENN-F-050509	TFB3772	Scotland	1, 2	MN413350	MW396885
Co. ramealis	TENN-F-067913	TFB14163h1	Germany: Thuringia	2	MN413351	—
Co. ramealis	TENN-F-067913	TFB14163h2	Germany: Thuringia	2	MN413352	—
Co. ramealis	TENN-F-067912	TFB14162h1	Germany	2	MN413353	—
Co. ramealis	TENN-F-067912	TFB14162h2	Germany	2	MN413354	—
Co. ramealis	TENN-F-067890	TFB14140c1	Germany: Thuringia	2	MN413355	—

Organism	Herbarium No.	Isolate	Location	Fig. no.	GenBank ITS	GenBank LSU
Co. ramealis	TENN-F-067890	TFB14140c2	Germany: Thuringia	2	MN413356	—
Co. ramealis	TENN-F-067890	TFB14140c3	Germany: Thuringia	2	MN413357	—
Co. ramealis	TENN-F-067890	TFB14140c4	Germany: Thuringia	2	MN413358	—
Co. ramealis	TENN-F-067890	TFB14140c5	Germany: Thuringia	2	MN413359	—
Co. ramealis	TENN-F-067890	TFB14140c6	Germany: Thuringia	2	MN413360	—
Co. ramealis	TENN-F-067890	TFB14140c7	Germany: Thuringia	2	MN413361	—
Co. ramealis	TENN-F-067890	TFB14140c8	Germany: Thuringia	2	MN413362	—
Co. ramealis	TENN-F-067900	TFB14150c1	Germany: Thuringia	2	MN413363	—
Co. ramealis	TENN-F-067900	TFB14150c2	Germany: Thuringia	2	MN413364	—
Co. ramealis	TENN-F-067900	TFB14150c3	Germany: Thuringia	2	MN413365	—
Co. ramealis	TENN-F-067900	TFB14150c7	Germany: Thuringia	2	MN413366	—
Co. ramealis	TENN-F-067900	TFB14150c8	Germany: Thuringia	2	MN413367	—
Co. ramealis	TENN-F-069255	TFB14559h1	Slovakia	2	MN413370	—
Co. ramealis	TENN-F-069255	TFB14559h2	Slovakia	2	MN413371	—
Co. ramealis	TENN-F-055908	TFB6989	Scotland	1, 2	MN413372	MW396883
Co. ramealis	BR 72_41	—	Belgium	1	MW396875	MW396875
Co. ramealis	TENN-F-069251	TFB14555	Slovakia	1, 2	MW405779	MW396884
Collybiopsis readiae						
Co. readiae	TENN-F-053687	TFB7571	New Zealand	1	DQ450034	—
Co. readiae	FZ1395	PDD:95844	New Zealand	1	HQ533036	—
Co. readiae	TENN-F-061061	TFB13056	New Zealand	1	KJ416244	—
Collybiopsis stenophylla						
Co. stenophylla	TENN-F-065943	TFB13998	USA: Tennessee, GSMNP	1, 2	MN413331	MW396886
Co. stenophylla	TENN-F-051099	TFB4798	USA: Georgia	1, 2	MN413330	MW396887
Co. stenophylla	TENN-F--059444	TFB11558	USA: North Carolina	2	DQ450032	—
Co. stenophylla	TENN-F--059449	TFB11559	USA: North Carolina	2	DQ450033	—
Collybiopsis subcyathiformis						
Co. subcyathiformis	URM 90023	—	Brazil: Para	1	KY404982	KY404982
Co. subcyathiformis	URM 90022	—	Brazil: Para	1	KY404983	KY404983
Collybiopsis subnuda						
Co. subnuda	TENN-F-061138	TFB12577	USA: Tennessee, GSMNP	1	KY026667	FJ750262

Organism	Herbarium No.	Isolate	Location	Fig. no.	GenBank ITS	GenBank LSU
Co. subnuda	WRW 08-462	—	USA: West Virginia	1	KY026765	KY026765
Co. subnuda	TENN-F-65984	TFB14043	USA: North Carolina	1	MW396876	MW396876
Collybiopsis trogioides						
C. trogioides [HT]	SFSU-AWW51	AWW51	Indonesia	1	AY263428	AY639431
"*Collybiopsis utriformis*"						
"*Co. utriformis*"	TENN-F-068185h1	TFB14334h1	USA: Connecticut	1	KY026707	KY026707
"*Co. utriformis*"	TENN-F-068185h2	TFB14334h2	USA: Connecticut	1	KY026708	KY026708
"*Co. utriformis*"	WRW05-1170	—	USA: West Virginia	1	KY026764	KY026764
Collybiopsis viallanti						
Co. viallanti	TENN-F-65115	TFB13739	USA: Tennessee, GSMNP	1	KY026676	KY026676
Collybiopsis villosipes						
Co. villosipes	TENN-F-056252	TFB9539	USA:	1	DQ450058	—
Co. villosipes	TENN-F-060951	TFB12836	New Zealand: Fiordland	1	KJ416255	FJ750264
Co. villosipes	iNaturalist	—	USA: California	1	MF163171	—
Collybiopsis* sp. *1						
Co. sp. 1	TENN-F-54944	TFB8605 culture	Argentina: Chubut	1	MW396870	MW396870
***Collybiopsis* sp. 2**						
Co. sp. *2*	TENN-F-051101	TFB4800	USA: Georgia	1	MW396874	MW396874
Gymnopanella nothofagi						
Gymnopanella nothofagi	SGO 163624	—	Chile	1	KT906424	KT906424
Gymnopanella nothofagi	SGO 163625	—	Chile	1	KT906425	KT906425
Gymnopus sp.						
Gymnopus VC-2017g	URM 90043	—	Brazil: Paraiba	1	KY321573	KY321573
Gymnopus VC-2017g	URM 90042	—	Brazil: Paraiba	1	KY321574	KY321574
Gymnopus VC-2017g	URM 90045	—	Brazil: Paraiba	1	KY321575	KY321575
Gymnopus sp.	environmental	olrim406	Sweden	1	KY352520	—
Gymnopus VC-2017g	URM 90054	—	Brazil: Paraiba	1	KY404984	—
Gymnopus sp.	FH: BHI-F523	BHI-F523a	USA: Maine, Peddocks Island	1	MF161290	—

Organism	Herbarium No.	Isolate	Location	Fig. no.	GenBank ITS	GenBank LSU
Mycetinis kallioneus						
My. kallioneus	GB-01505113	—	Norway: Svalbard	1	KX958397	KX958397
Mycetinis opacus						
My. opacus	TENN-F-060016	TFB11787	USA: Tennessee, GSMNP	1	KY696758	KY696758
My. opacus	TENN-F-069200	TFB14490h1	USA: Mississippi	1	KY696768	KY696768
My. opacus	TENN-F-069200	TFB14490h2	USA: Mississippi	1	KY696769	KY696769
My. opacus	TENN-F-054871	TFB9071	USA: Mississippi	1	MW396877	MW396877
My. opacus	BM071315-2	Bruce Macol 888	USA: Tennessee	1	MW396878	MW396878
Mycetinis salalis						
My. salalis	DAOM:175251	—	—	1	KX752265	KX752265
Mycetinis scorodonius						
My. scorodonius	TENN-F-050522	TFB3785	Sweden: Vastergotland	1	KY696731	KY696731
My. scorodonius	TENN-F-050689	TFB3701	USA: North Carolina	1	KY696733	KY696733
My. scorodonius	TENN-F-050696	TFB3708	USA: Tennessee, GSMNP	1	KY696734	KY696734
My. scorodonius	TENN-F-051442	TFB5031	Canada: Nova Scotia	1	KY696739	KY696739
My. scorodonius	TENN-F-053466	TFB4969	USA: New York	1	KY696741	KY696741
My. scorodonius	TENN-F-053467	TFB5025	Canada: Nova Scotia	1	KY696742	KY696742
My. scorodonius	TENN-F-053471	TFB4939	USA: New York	1	KY696746	KY696746
My. scorodonius	TENN-F-053474	TFB5005	USA: Maine	1	KY696748	KY696748
Paramycetinis austrobrevipes						
P. austrobrevipes [HT]	TENN-F-050135	TFB4033	Australia: Tasmania	1	KY026622	KY026622
P. austrobrevipes	TENN-F-053149	TFB3591	Australia: Tasmania	1	KY026637	KY026637
P. austrobrevipes	TENN-F-053181	TFB3585	Australia: Tasmania	1	KY026638	KY026638
Paramycetinis caulocystidiatus						
P. caulocystidiatus	TENN-F-053683	TFB7572	New Zealand	1	KY026642	KY026642
P. caulocystidiatus	TENN-F-053721	TFB7588	New Zealand	1	KY026643	KY026643
P. caulocystidiatus	TENN-F-053725	TFB7589	New Zealand: North Island	1	KY026644	KY026644
P. caulocystidiatus [HT]	TENN-F-054050	TFB7148	New Zealand	1	KY026645	KY026645

Materials & methods

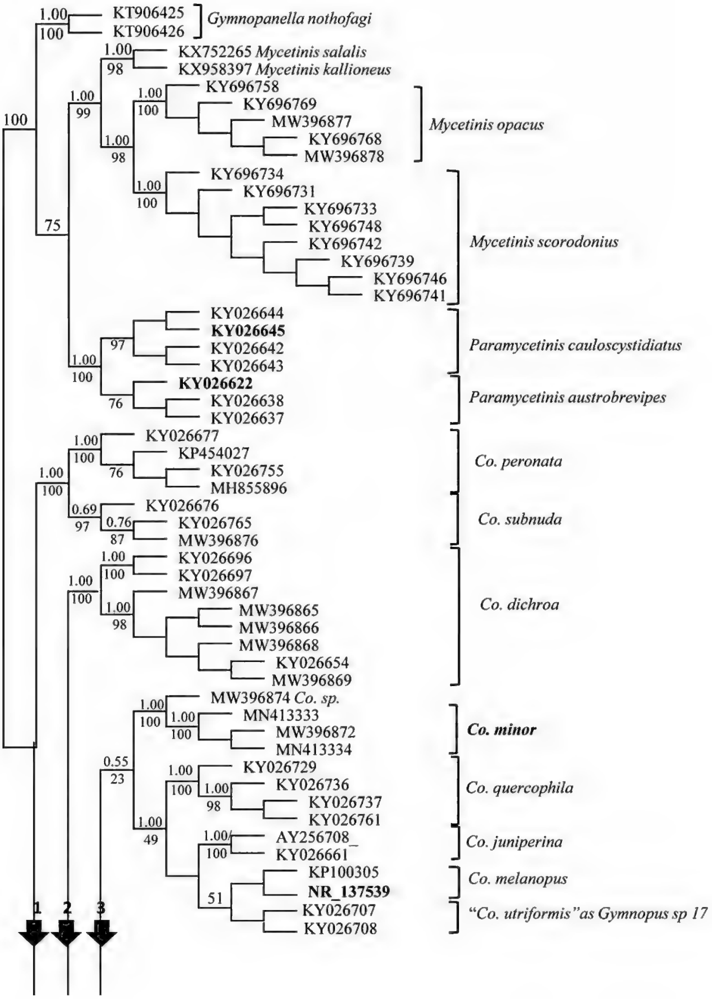
Abbreviations: Throughout this paper, *Co* = *Collybiopsis*; *G* = *Gymnopus*; *M* = *Marasmius*; *Ma* = *Marasmiellus*. Colors cited alphanumerically are from Kornerup & Wanscher (1967) and those in quotation marks are from Ridgway (1912). BF = bright field microscopy; PhC = phase contrast microscopy (see also Petersen & Hughes 2017b). TFB = Tennessee field-book number, assigned to fresh collections in order to track specimen, photos, notes, etc.; TENN-F-XXXXXX = official designation of the herbarium of the University of Tennessee (and Mycoportal number). GSMNP = Great Smoky Mountains National Park. In basidiospore metrics, E = range of spore lengths divided by spore widths; E^m = median spore length divided by median spore width; L^m = median spore length. In descriptions L = complete lamellae; L + ll = lamellae + lamellulae Herbarium acronyms are from Index Herbariorum.

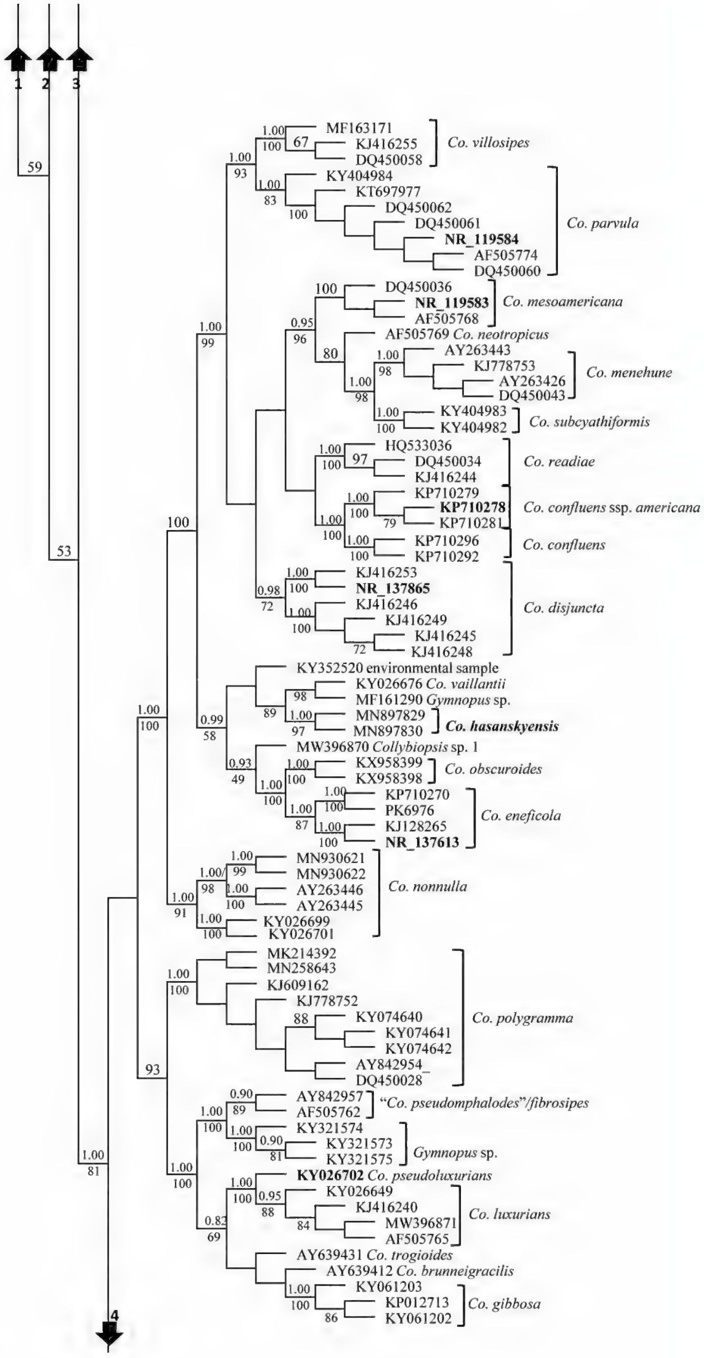
Metrics of microstructures were calculated using an Olympus BX60 microscope fitted with phase contrast imagery and photographs of microstructures were produced with an Olympus Q_c color camera. Microscope mounts were usually in 3% KOH solution or Melzer's reagent (abbr. IKI).

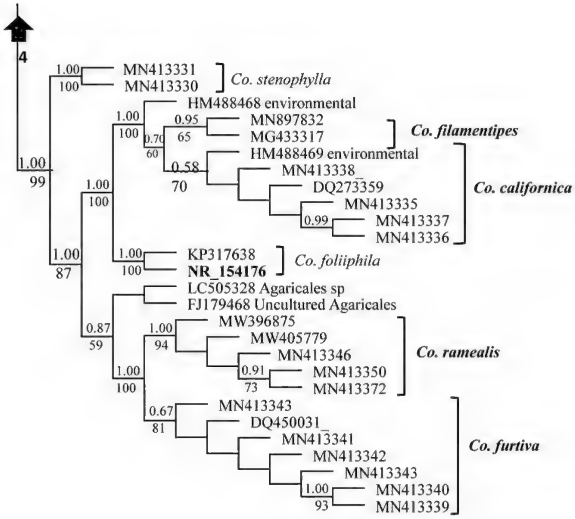
Molecular methods for DNA extractions, PCR, and Sanger sequencing of the nuclear ribosomal ITS and LSU regions were described in Aldrovandi et al. (2015). DNA sequence alignments with concatenated ITS and LSU sequences (where available (see Table 1) were performed in Geneious 11.0.3 (2017) using Clustal W (Thompson & al. 1994) then manually adjusted in AliView 1.26 (Larsson 2014). Unlike Olivera & al., (2019), we did not delete highly variable regions of the alignment because information content in these regions informed species groupings. PhyML phylogenetic analyses were performed in Geneious 11.0.3 (2017) using a Generalized Time-reversable model (GTR) with 4 nucleotide substitution rate catigories and a gamma rate variation with 4 categories. Values for the transition/transversion ratio, proportion of invariable sites, and gamma distribution parameter were estimated. 500 boot strap replications were performed. Bayesian analysis was performed in Geneious 11/0/3 using MrBayes 3.2.6 (Huelsenbeck & Ronquist 2001) with a GTR model of evolution, 4 chains and a burn-in of 100,000. Chain length was 1,100,000. Sequences were deposited in GenBank (Table 1). Specimen data are available in Mycoportal (MyCoPortal 2018).

Taxonomy

An ITS+LSU phylogeny of *Collybiopsis* is presented in Fig. 1. *Gymnopanella nothofagi*, *Mycetinis* spp., and *Paramycetinis* spp. were selected as related outgroups based on a nrLSU phylogeny in Petersen & Hughes (2020). *Collybiopsis* as circumscribed in this paper includes *Co. dichroa*, a genetic complex of several poorly circumscribed taxa. *Collybiopsis dichroa* I and II form natural hybrids but there is no evidence that F2 later progeny are viable (Hughes & al. 2015). *Collybiopsis ramealis* appears as sister to *Co. furtiva* and is in a larger, well-supported clade with *Co. stenophylla, Co. filamentipes, Co. californica,* and *Co. foliiphila.*




1
2
3
59
53
1.00
81
MF163171
1.00
100
67
KJ416255
DQ450058
Co. villosipes
1.00
93
KY404984
1.00
83
KT697977
100
DQ450062
DQ450061
NR_119584
AF505774
DQ450060
Co. parvula
1.00
99
100
DQ450036
NR_119583
AF505768
Co. mesoamericana
0.95
96
AF505769 Co. neotropicus
80
1.00
98
AY263443
KJ778753
1.00
98
AY263426
DQ450043
Co. menehune
1.00
100
KY404983
KY404982
Co. subcyathiformis
1.00
100
HQ533036
97
DQ450034
KJ416244
Co. readiae
1.00
100
KP710279
KP710278
79
KP710281
Co. confluens ssp. americana
1.00
100
1.00
100
KP710296
KP710292
Co. confluens
100
53
1.00
100
KJ416253
NR_137865
0.98
72
1.00
100
KJ416246
KJ416249
KJ416245
72
KJ416248
Co. disjuncta
KY352520 environmental sample
KY026676 Co. vaillantii
98
MF161290 Gymnopus sp.
89
1.00
97
MN897829
MN897830
Co. hasanskyensis
1.00
100
0.99
58
MW396870 Collybiopsis sp. 1
0.93
49
1.00
100
KX958399
KX958398
Co. obscuroides
1.00
100
1.00
100
KP710270
PK6976
1.00
87
1.00
100
KJ128265
NR_137613
Co. eneficola
1.00
99
MN930621
MN930622
1.00/
98
1.00
100
AY263446
AY263445
1.00
91
1.00
100
KY026699
KY026701
Co. nonnulla
MK214392
MN258643
1.00
100
KJ609162
KJ778752
88
KY074640
KY074641
KY074642
AY842954
DQ450028
Co. polygramma
93
0.90
89
AY842957
AF505762
"Co. pseudomphalodes"/fibrosipes
1.00
100
1.00
100
KY321574
0.90
81
KY321573
KY321575
Gymnopus sp.
1.00
100
KY026702 Co. pseudoluxurians
1.00
100
0.95
88
KY026649
KJ416240
84
MW396871
AF505765
Co. luxurians
0.82
69
AY639431 Co. trogioides
AY639412 Co. brunneigracilis
1.00
100
KY061203
86
KP012713
KY061202
Co. gibbosa
4



Figs 1A, B, C. PhyML tree of concatenated nrITS and LSU *Collybiopsis* sequences. Support values at the nodes consist of Bayesian posterior probabilities (top value) and PhyML bootstrap support based on 500 replications (bottom value). The outgroup comprises *Gymnopanella* and *Mycetinis*. The label on each branch represents the nrITS GenBank accession number. Corresponding LSU sequences are given in Table 1. GenBank accession numbers in bold represent types. Taxa described in this paper are also in bold. The phylogeny is divided into three parts with arrows connecting each part.

An nrITS-based phylogeny including all sequenced collections of *Co. ramealis* (Fig. 2) demonstrates that *Co. ramealis* represents a complex, not a single taxon. Several issues are resolved or raised. First, European collections are very nearly homogeneous based on nrITS sequences, so topotype *Co. ramealis* remains a circumscribable taxon well described by Antonín & Noordeloos (2010) and below. Examination of nrITS sequences reveals, however, that the European population consists of two ITS haplotypes and hybrids, with indications that genetic recombination has occurred between haplotypes. Conversely, at least some North American collections (to this time limited to southeastern North America), are clearly separated from *Co. ramealis,* and are here described as *Co. furtiva.* Likewise, *Marasmiellus ramealis* var. *californicus* lies within *Collybiopsis*, discrete at species rank and more widely distributed than anticipated.

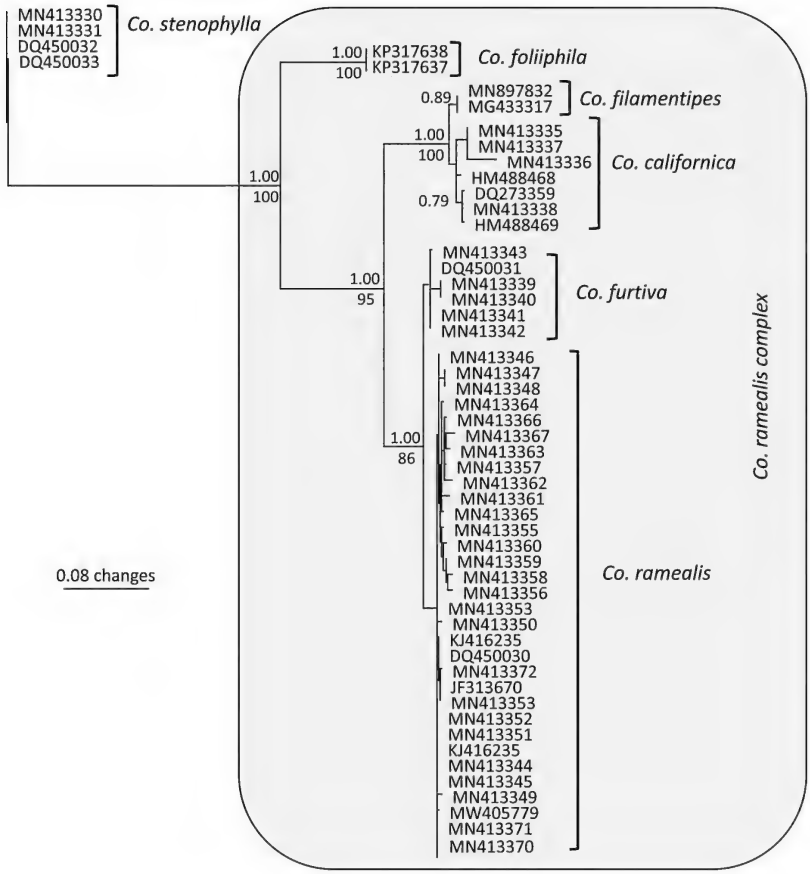


Fig. 2. PhyML tree of nrITS sequences representing the *Collybiopsis ramealis* complex. *Collybiopsis stenophylla* was used as an outgroup. Support values at the nodes consist of Bayesian posterior probabilities (top value) and PhyML bootstrap support based on 500 replications (bottom value). The label on each branch represents the nrITS GenBank accession number.

Taxonomic analyses

Collybiopsis californica (Desjardin) R.H. Petersen, **stat. nov.** Figs 3–13

IF 556204

Basionym: *Marasmiellus ramealis* var. *californicus* Desjardin, Mycologia 79: 132. 1987.

Holotype: USA, California, Los Angeles Co., San Dimas, 34°06′23″N 117°48′25″W, 9.III.1983, Wright 2941 (SFSU-F s.n.).

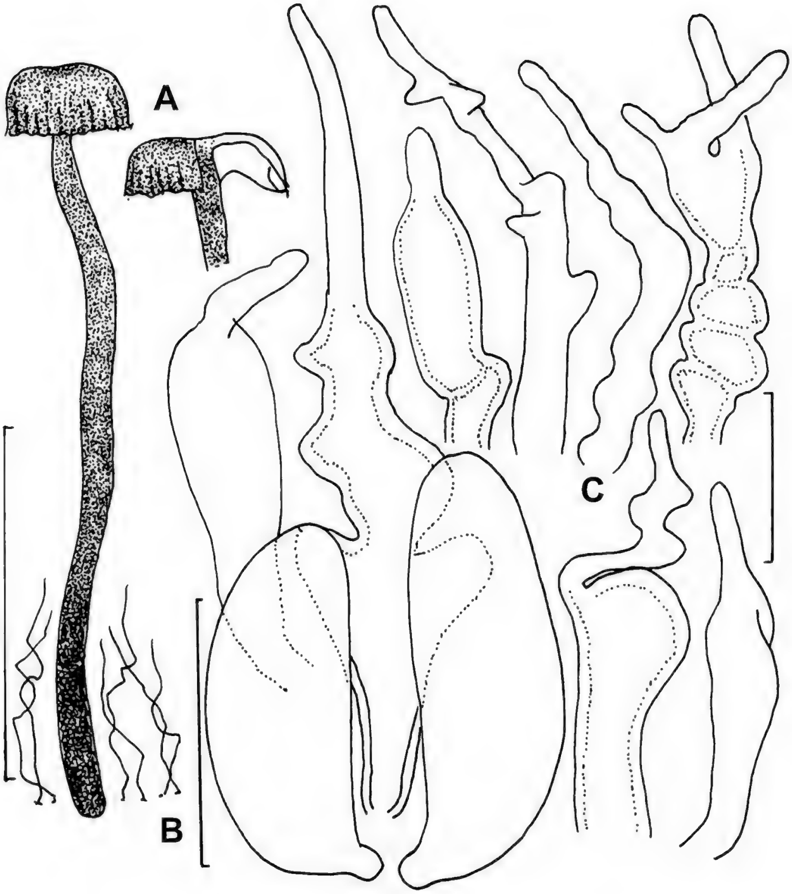


Fig. 3. *Collybiopsis californica* (Wright 866; SFSU–F-024539).
A. Basidiomata and rhizomorphs. B. Basidiospores. C. Termini of caulocystidia.
Scale bars: A = 10 mm; B = 5 µm; C = 10 µm.

Desjardin (1987) offered a detailed, comprehensive description of *Marasmiellus ramealis* var. *californicus*. Our Fig. 2 indicates that the taxon, while related to *Co. ramealis* (both European and putative American), is separable from *Co. ramealis* at species rank, triggering the rank change above. The following items are worthy of note: 1) photographic images and discussion of microstructures (Figs 3–13); and 2) the taxon's apparent extended geographic distribution.

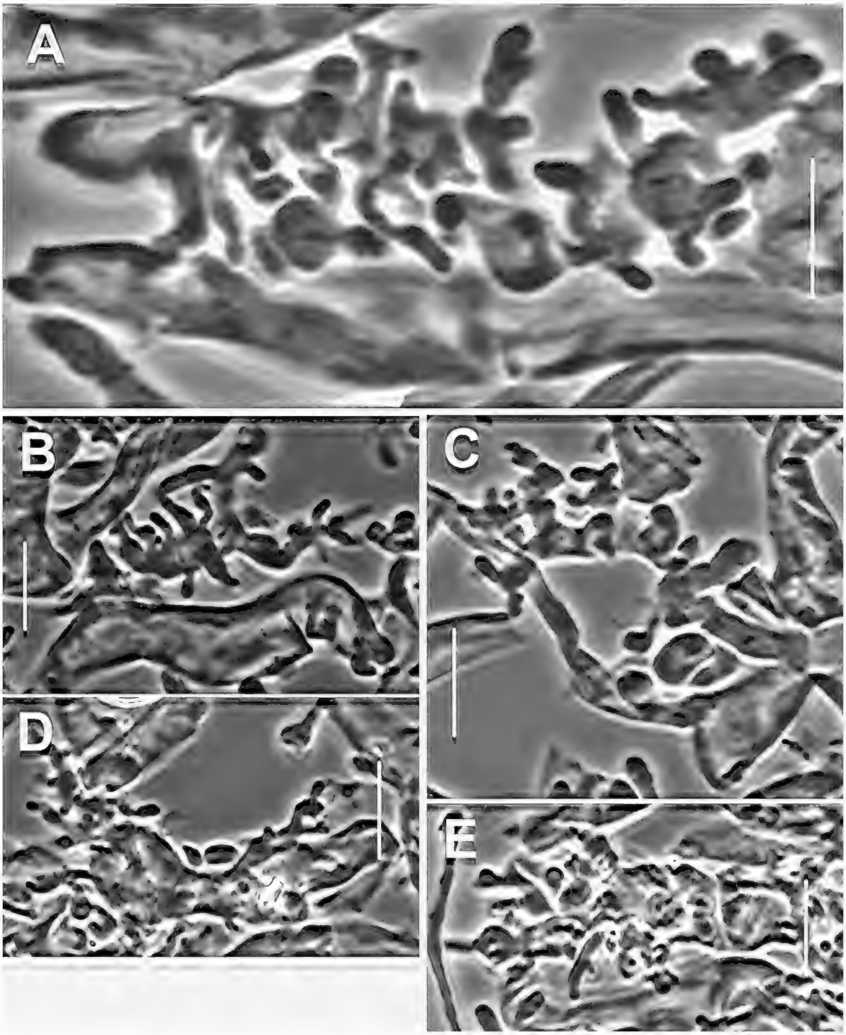


Fig. 4. *Collybiopsis californica*. (Wright 2941 SFSU s.n.).
Diverticulate pileipellis hyphae. Scale bars = 10 µm.

A comparison of microstructures of *Co. californica* (Figs 3–13) with those of *Co. ramealis* (Figs 50–60) includes the nature of the structure of pileipellis hyphae. In *Co. ramealis*, diverticula are slender, digitate and appear rigid, while those of *Co. californica* (Fig. 5) are broad, often fin- or node-like, gnarled and repeatedly branched. Pleurocystidia (Fig. 6), basidioles, and basidia (Fig. 7)

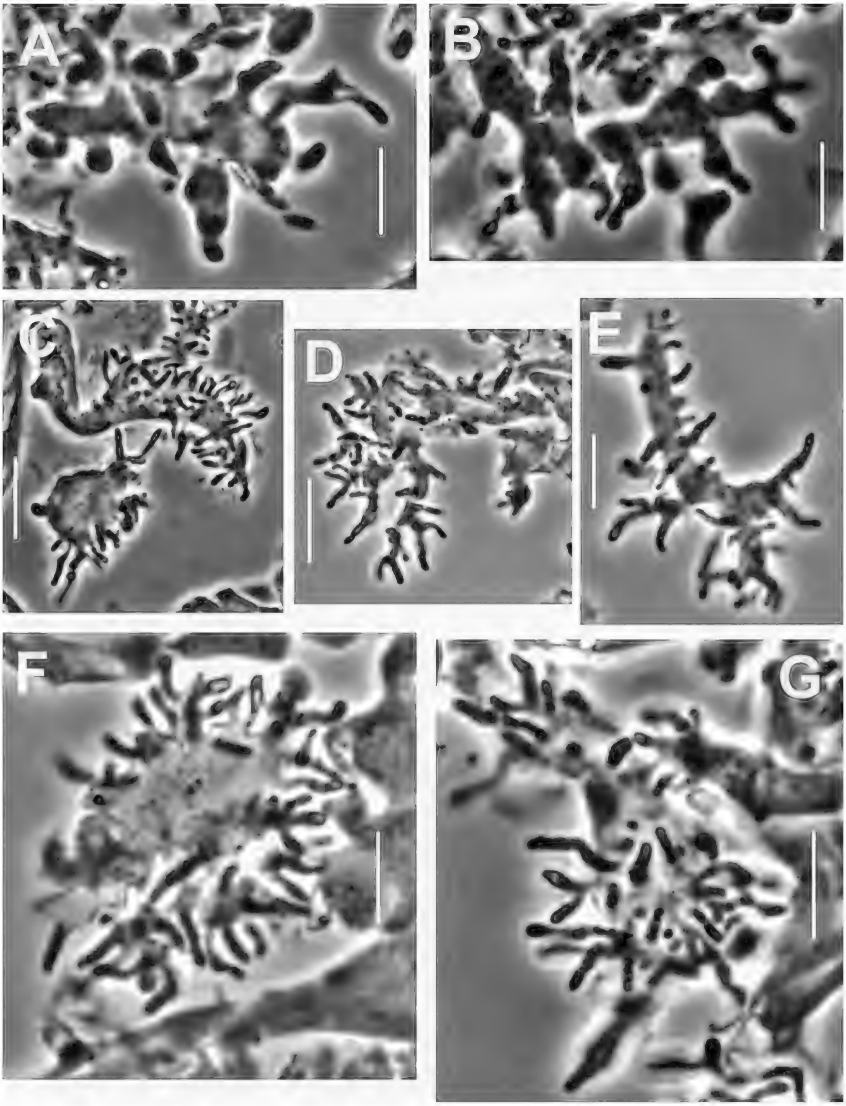


Fig. 5. *Collybiopsis californica*. (TFB 5787; TENN-F-052617). Pileipellis elements. A, B. Lobate-diverticulate elements. C-G. Diverticulate elements.

are similar to those of *Co. ramealis*, although somewhat longer. The variability of cheilocystidial shape from broadly clavate to ventricose-rostrate (Figs 8–11) is notable, but lengths and breadths of diverticula (which are often

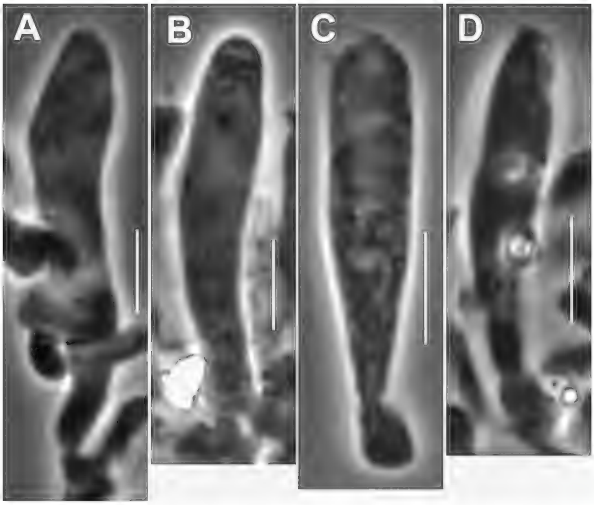


Fig. 6. *Collybiopsis californica*. (Wright 866; SFSU–F-024539). Pleurocystidia. Scale bars = 10 µm.

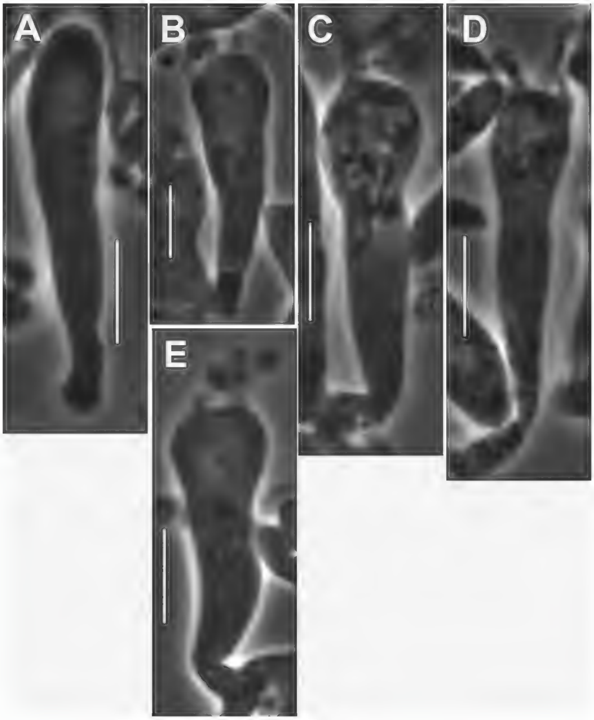


Fig. 7. *Collybiopsis californica* (Wright 2941; SFSU s.n.).
A. Basidiole. B-E. Basidia. Scale bars = 10 µm.

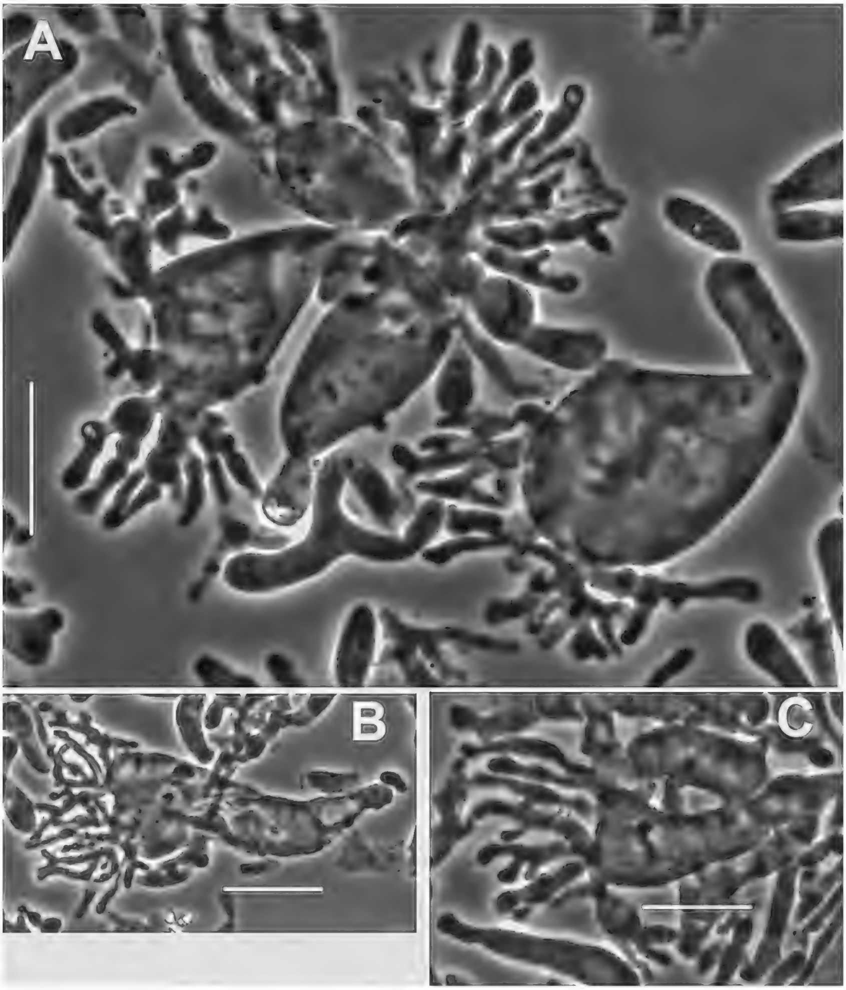


Fig. 8. *Collybiopsis californica*. (Wright 2941; SFSU s.n.). Cheilocystidia. A. Cluster of three individuals. B, C. Individual cheilocystidia. Scale bars = 10 µm.

subcapitate) are much longer and stouter. More intriguing, cheilocystidia of *Co. californica* are often transversely septate (apparently non-clamped; Figs. 11) and apparently easily disarticulated at this septum. The result is frequent subglobose to ventricose diverticulate structures with no evidence of stalk. Whether these structures could act as propagules is unknown. Finally, caulocystidia predictably range from short, simple, individual lobes at upper stipe (Figs 12, 13) to mid- or lower stipe vesture comprising

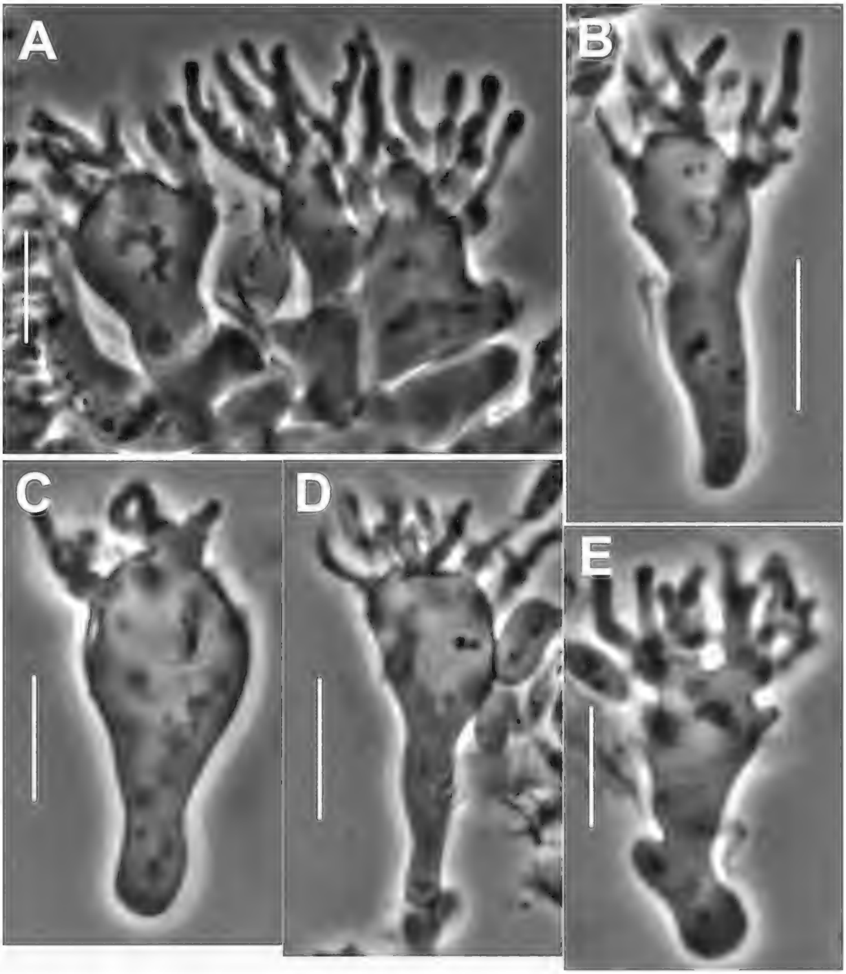


Fig. 9. *Collybiopsis californica*. (DED 8372; SFSU-F-024526). Cheilocystidia. A. Cluster of three individuals. B-E. Individual cheilocystidia.

fascicles of hyphae perpendicular to stipe surface. Smaller such fascicles (Fig. I3) are synnematoid while larger assemblages are acervuloid.

At the time of initial proposal, all collections of *Co. californica* had been gathered in southern California. Since then, samples of mycelial mats under *Pseudotsuga menziesii* in northern California and roots of *Lithocarpus densiflorus* in Oregon have yielded sequences quite similar to those of the southern Californian collections (Bergemann & Garbelotto

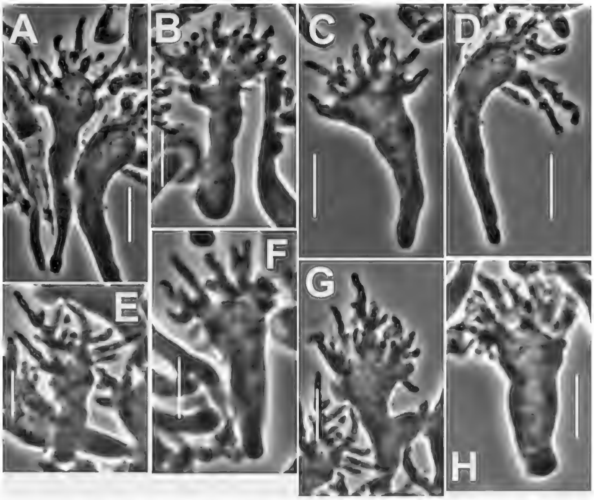


FIG. 10. *Collybiopsis californica*. (TFB 5787; TENN-F-052617). Cheilocystidia. Scale bars = 10 µm.

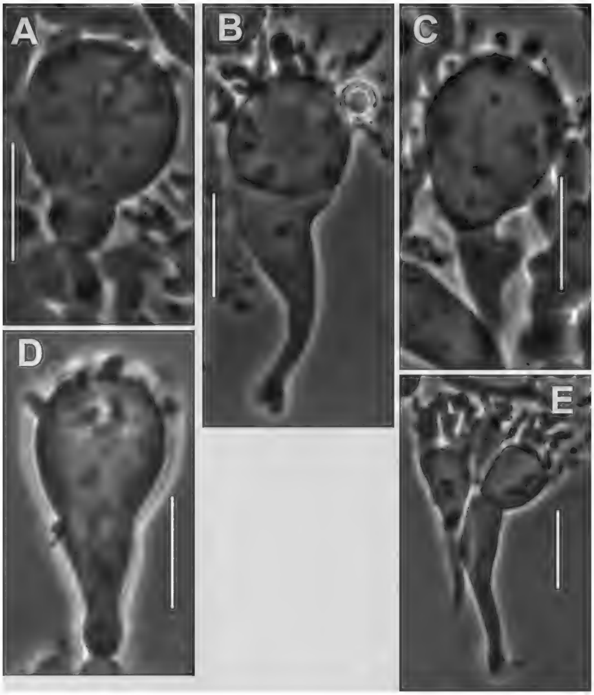


FIG. 11. *Collybiopsis californica*. (DED 8372; SFSU-F-024526). Cheilocystidia. A. Constricted by not septate cheilocystidium. B, C, E. Septate cheilocystidia. D. Cheilocystidium with septum below constriction. Scale bars = 10 µm.

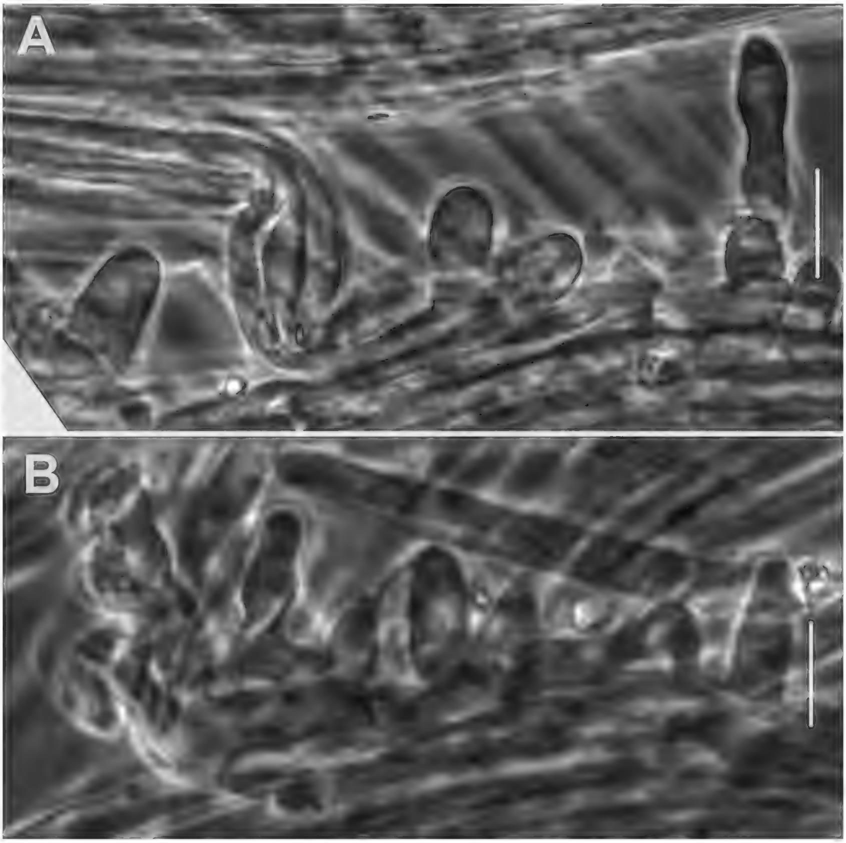


Fig. 12. *Collybiopsis californica*. (DED 8372; SFSU-F-024526). Upper stipe ornamentation; individual nodose, digitate caulocystidia. Scale bars = 10 µm.

2006; Kluber & al. 2011). Likewise, a sequence from a British Columbian collection (Canada, TENN-F-052617) matches the Californian collections. The species, obviously, exhibits a much wider distribution than originally conceived.

Pileipellis hyphal morphology is reminiscent of that of *Gymnopus pyracanthoides* (Petersen & Hughes 2016), especially regarding the complexity of diverticulate hyphae and broom cell-like termini of pileipellis hyphae. Basidiomata of the latter species, however, exhibit a slime matrix in the stipe medulla and the pileipellis includes some scanty evidence of gelatinous matrix, placing it in *Gymnopus* sect. *Perforantes*.

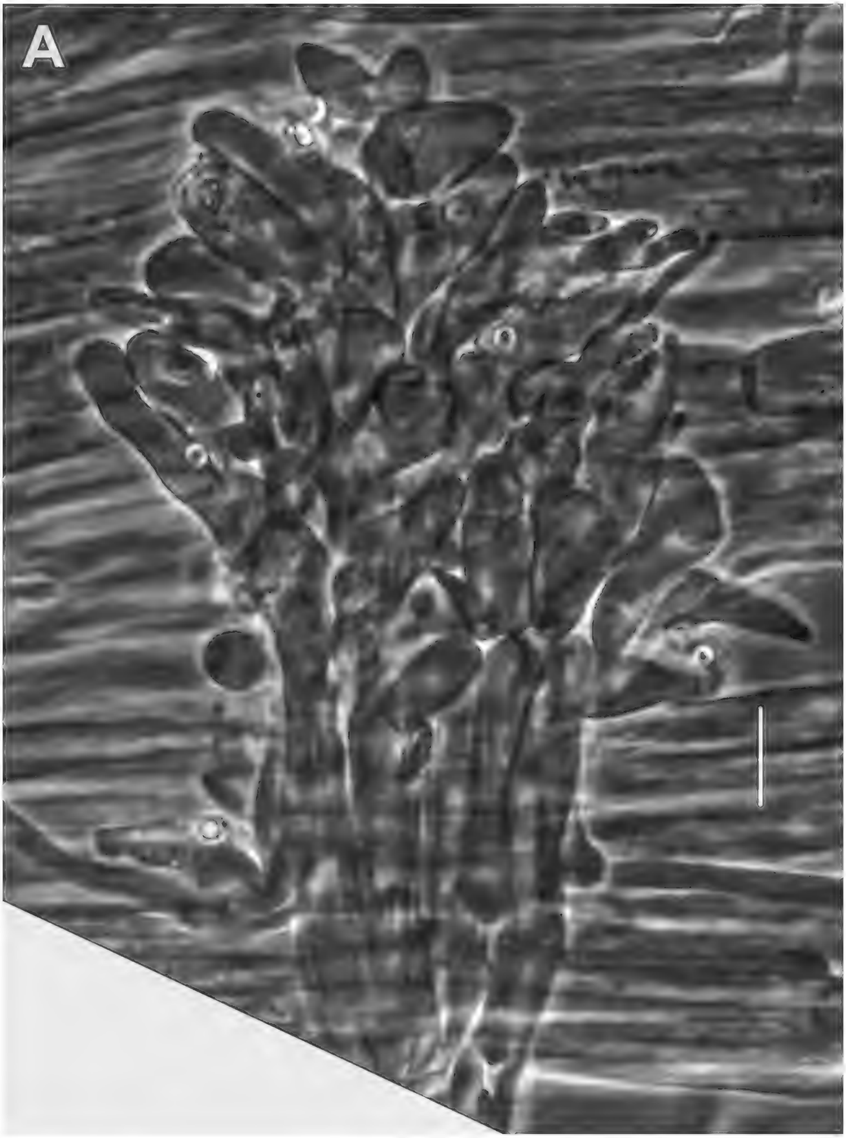


Fig. 13. *Collybiopsis californica*. (DED 8372; SFSU-F-0024526). Mid-stipe ornamentation. Synnematoid fascicle of caulocystidia. Scale bar = 10 µm.

Additional specimens examined: **CANADA**, **British Columbia**, Chilliwack River Valley, 49°09′38″N 121°57′02″W, 8.X.1992, coll. RHP (as *Marasmius androsaceus*), TFB 5787 (TENN-F-052617). **USA**, **California**, **Los Angeles Co.**, Marshall Canyon, 34°06′23″N 117°48′25″W, 12.I.1978, coll. G Wright, det. DE Desjardin, Wright 866 (SFSU-F-024539); **Marin Co.**, Point Reyes Nat. Seashore, Horse Trail, 38.043191 N, 122.802687, Wright 2941 (SASFU s.n.); , W, 11.XI.2008, coll. & det. DE Desjardin, DED 8372 (SFSU-F-024526); **Trinity Co.**, Rte 299. Grey's Falls Campground,40°51′26″N 123°29′30″W, 15.XI.1999. coll. D Largent, TFB 8088 (TENJN-F-055412).

Collybiopsis filamentipes R.H. Petersen, **sp. nov.** Figs. 14-23

IF 557073

Differs from *Co. furtiva* in its narrower basidiospores, its caulocystidial shape and distribution, and its longer and thinner stipe.

Type: USA, Tennessee, Knox Co., Knoxville, 3613 Timberlake Dr., 35°54′49″N 83°57′58″W, 22.VIII.2011, coll. RHP, TFB 13962 (**Holotype**, TENN-F-065861).

Etymology: Referring to the long, slender stipe.

Basidiomata (Fig. 14A, 15) diminutive, gracile, decidedly mycenoid. Pileus 2–11 mm broad, strongly convex when young, later shallowly convex, matt; disc near "pinkish buff" 6A3, outward somewhat paler, hardly changing color upon drying. Lamellae adnexed to subdecurrent, few (L + ll = 12–13; L = 0–1), thickish with rounded edge with no anastomoses or buttressing, subventricose, off-white, developing pastel cantaloupe necropigment upon drying. Stipe 12–21 × 0.5–1 mm, concolorous with lamellae above, slightly darker downward but never darker than "sayal brown" 6C5 developing cantaloupe colored necropigment upon drying, not insititious, upward sometimes subsaccharine, downward almost glabrous. Taste and odor negligible. Rhizomorphs absent.

Habitat & distribution: apparently associated with *Poaceae* (lawn grass, dead fine roots of ornamental bamboo); so far extremely restricted to a small area of eastern Tennessee; mid-summer. Known only from the type locality with two collections (1970, 2011).

Pileipellis constructed of three elements with intermediate forms: 1) repent, inflated, free-form hyphae <14 µm diam, firm-walled, inconspicuously clamped (due to hyphal inflation), barely roughened to distinctly encrusted in small, densely gregarious patches – no annular or helical patterns observed, with frequent secondary septa (cloissons de retret) (Figs.16, 17); 2) repent hyphae as in 1) but beset with diverticulate to setuloid ornamentation (Fig.18C); setulae <6 × 1–1.5 µm; diverticula <9 × 1–2.5 µm at base, lobate to conical, simple to variously branched;

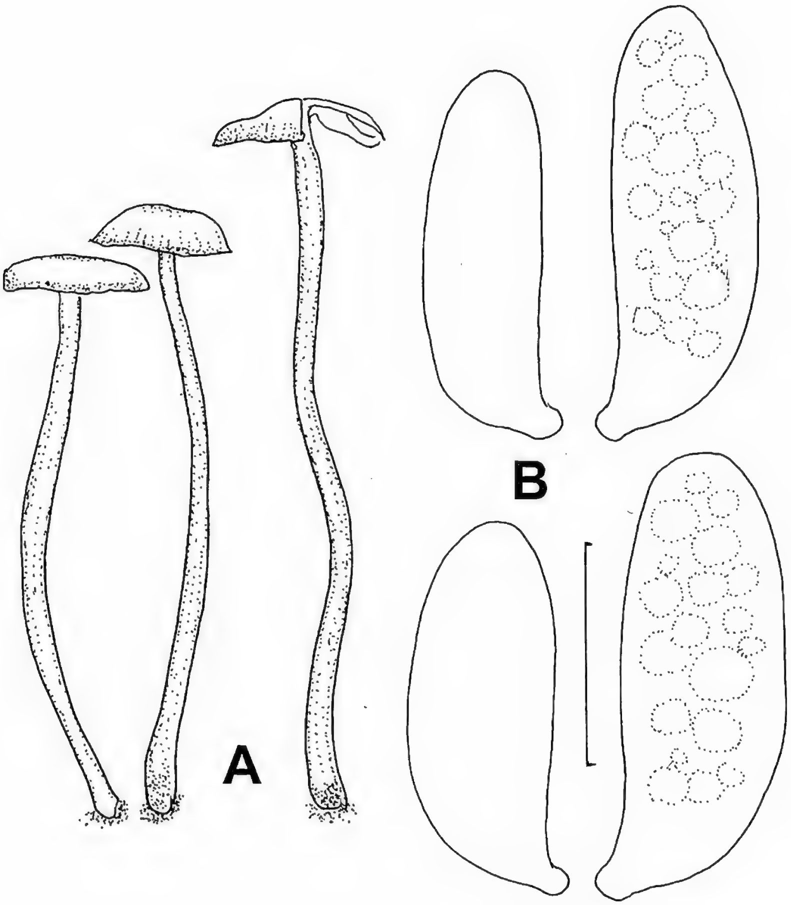


Fig. 14. *Collybiopsis filamentipes*. A. Basidiomata. (TFB 13962; TENN-F-065861). B. Basidiospores (upper = TFB 13962; lower = LRH 35861). Scale bar = 5 µm (for spores); 5 mm (for basidiomata).

and 3) hyphal termini (Fig 18A, B, D) as in 2), usually antler-branched and with setulae and/or diverticula. Pileus and lamellar trama interwoven; hyphae 3–13 µm diam, thin- to firm-walled, conspicuously clamped. Pleurocystidia (Fig. 19) 25–32 × 6–8 µm, stalked-fusiform, rounded apically, inconspicuously clamped; contents multigranular or multiguttulate,

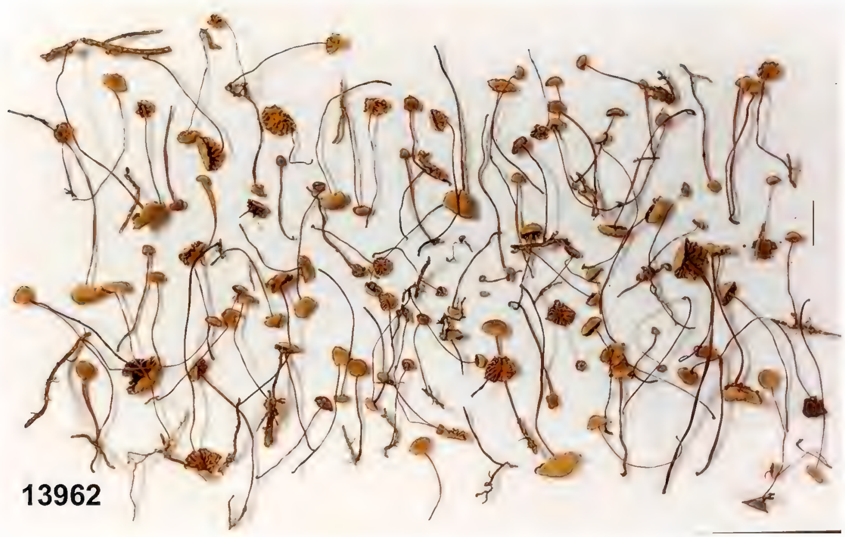


Fig. 15. *Collybiopsis filamentipes*. (TFB 13962; TENN-F-065861). Basidiomata (dried). Scale bar = 10 mm.

occasionally partitioned. Basidia 26–33 × 7–8 µm, clavate, 4-sterigmate, inconspicuously clamped; contents multiguttulate, usually with one major distal guttule. Basidiospores (Fig. 14B) 8–9.5(–10.5) × 2.5–3.5 µm (E = 2.29–3.80; E^m = 2.96; L^m = 8.8 µm), cylindrical to elongate-ellipsoid, thin-walled, smooth, inamyloid; contents multiguttulate, the guttules usually bipolar. Lamellar edge composed of two elements: 1) cheilocystidia (Figs. 20, 21A–C) plentiful, typically clavate to broadly clavate, 35–70 × 8–18(–25) µm, occasionally stoutly dichotomous, conspicuously clamped, hyaline, firm-walled, surmounted by numerous diverticula; diverticula 3–15 × 1.5–2 µm, appearing flexuous (not rigid), often branched, sometimes repeatedly so; and 2) diverticulate hyphae (Fig. 21D, E, 22) 5–8 µm diam, firm-walled with diverticula in files; diverticula as in 1) above. Stipe medullary hyphae (2–)3.5–7.5 diam, hyaline, embedded in a slime matrix, strictly parallel, thick-walled (wall <1.5 µm thick, hyaline), inconspicuously clamped. Stipe cortical hyphae 2–6.5 µm diam, thick-walled (wall 1.5 µm thick, golden ochre), inconspicuously clamped, producing hyphal termini and side branches (caulocystidia) perpendicular to stipe surface.

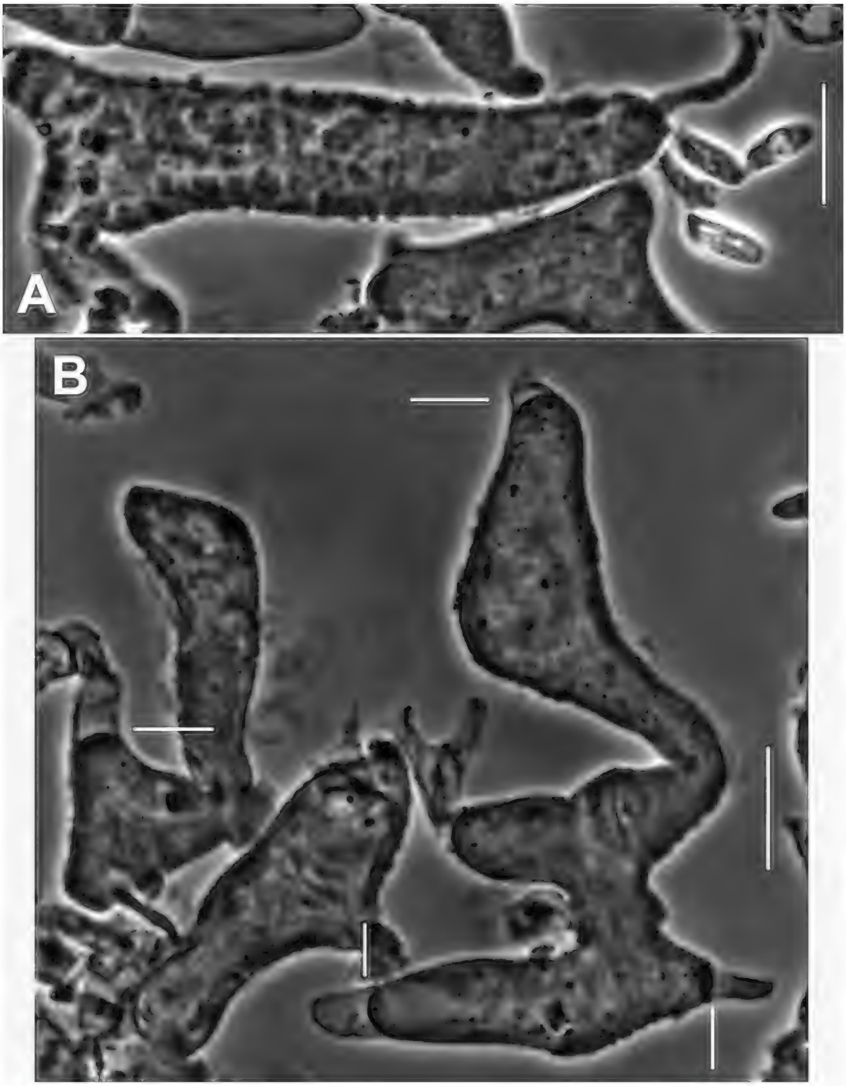


Fig. 16. *Collybiopsis filamentipes.* (TFB 13962; TENN-F-065861). Pileipellis.
A. Intricately encrusted hypha with apical diverticulate outgrowth. Note basidiospores.
B. Free-form hyphae. Short lines indicate secondary septa.
Scale bars = 10 µm.

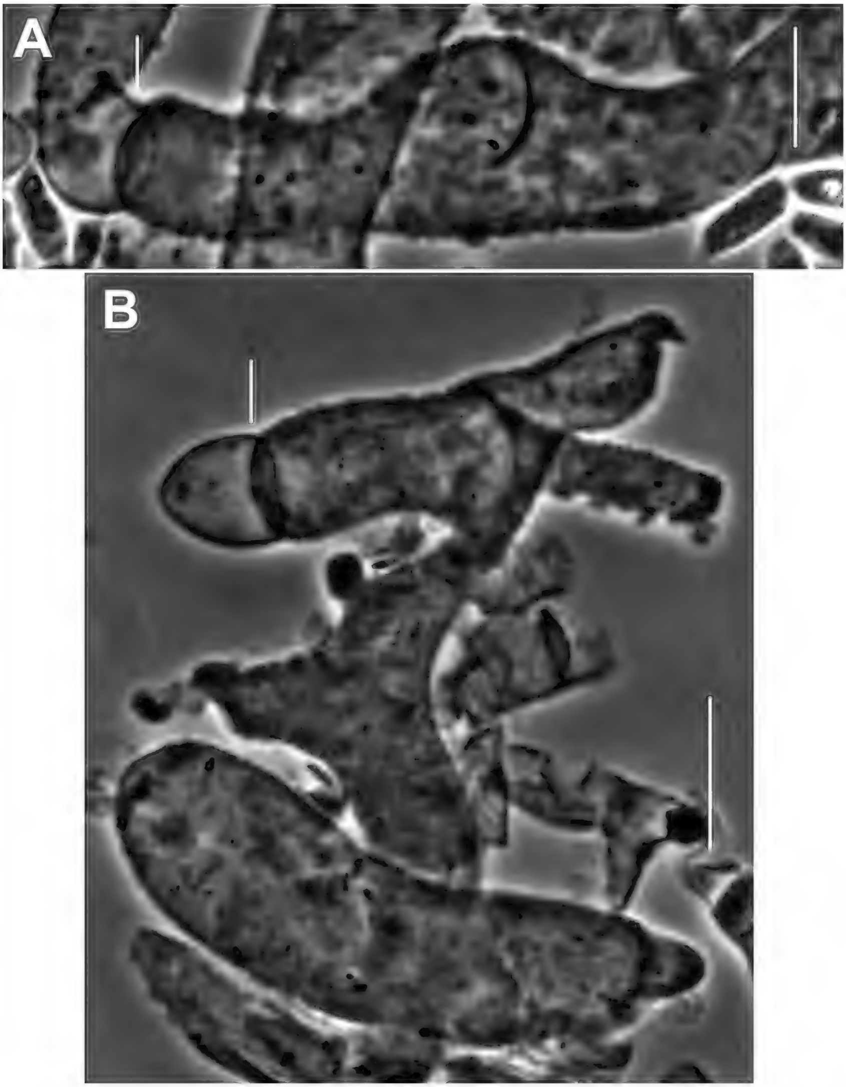


Fig. 17. *Collybiopsis filamentipes.* (TFB 13962; TENN-F-065861). Pileipellis.
Inflated, repent hyphae with moderate encrustation.
Short lines indicate secondary septa.
Scale bars = 10 μm.

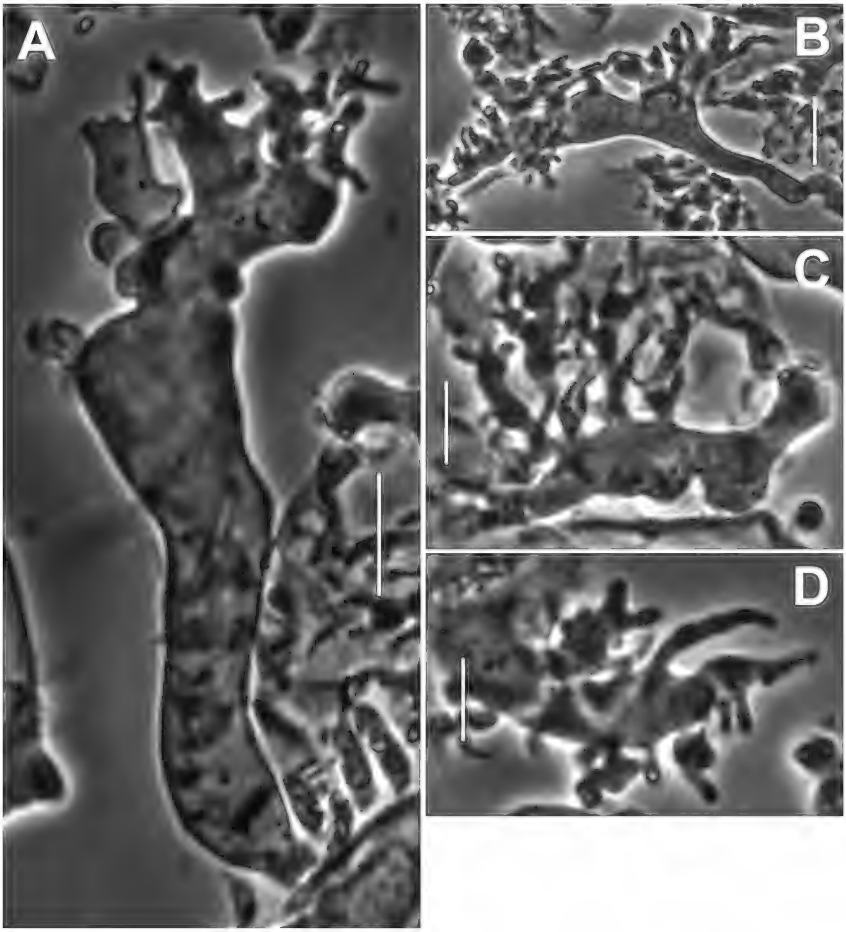


Fig. 18. *Collybiopsis filamentipes.* (TFB 13962; TENN-F-065861). Pileipellis. Diverticulate hyphae. A. Inflated hypha with apical diverticula. B, D. Hyphal terminus with diverticula. C. Diverticulate hypha. Scale bars = 10 µm.

Caulocystidia (Fig. 23) 5–20(–40) × 6–9 µm, columnar to digitate, rarely branched, firm-walled, hyaline, without clamp connections, detersile.

Commentary: Basidiomata of *Co. filamentipes* resemble those of *Co. furtiva*, a southeastern American species in the *Co. ramealis* complex. An even closer molecular match (~99%) is with *Co. californica*, distributed along the

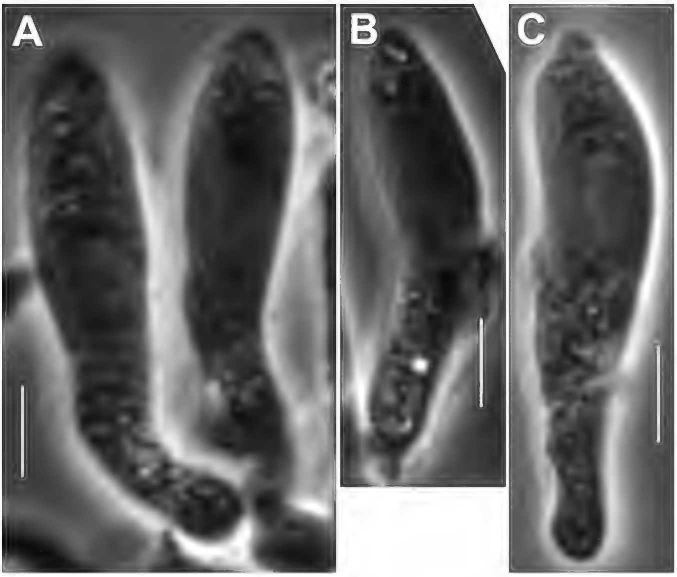


Fig. 19. *Collybiopsis filamentipes*. (TFB 13962; TENN-F-065861). Pleurocystidia. Scale bars = 10 µm.

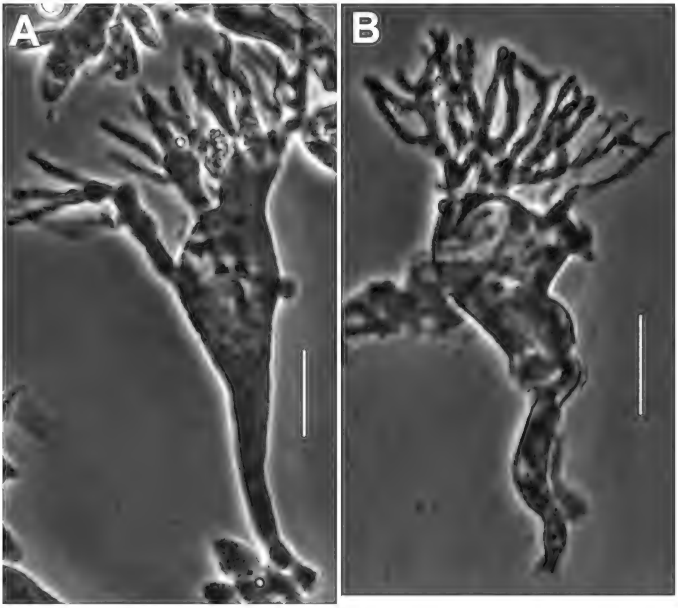


Fig. 20. *Collybiopsis filamentipes*. (TFB 13962; TENN-F-065861). Cheilocystidia. Scale bars = 10 µm.

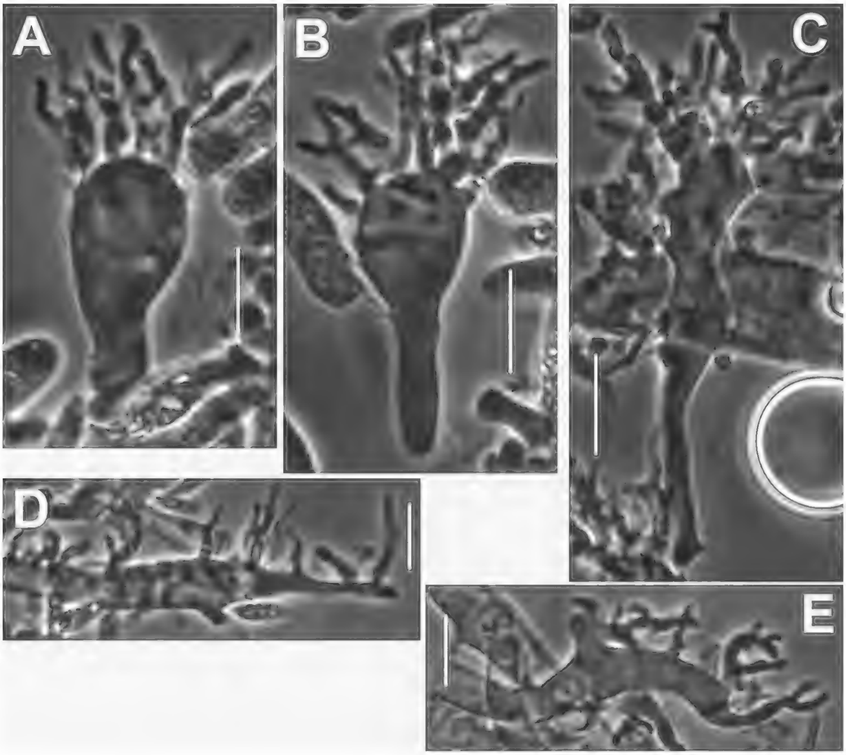


Fig. 21. *Collybiopsis filamentipes*. (TFB 13962; TENN-F-065861). Cheilocystidia.
A-C. Typical forms with apical diverticula.
D, E. Diverticulate hyphae of the hymenium.
Scale bars = 10 µm.

North American west coast. *Collybiopsis filamentipes* shares with both inflated cells in the pileipellis, *Rameales*-structure pileipellis, cheilocystidia bearing long tentacular diverticula, spore shape (*Co. furtiva* spores slightly wider than those of *Co. filamentipes*) and caulocystidia shape and distribution. Basidiomatal stature is surely different; stipe (and therefore the stipe length to pileus breadth ratio) is much longer and thinner in *Co. filamentipes* than in *Co. furtiva* and *Co. californica*.

Collybiopsis filamentipes adds to the *Co. ramealis* clade, species of which exhibit small micromorphological differences separable only with molecular techniques and/or a careful and practiced eye. As in other such compact clades, geographical distributions seem to support micromorphological

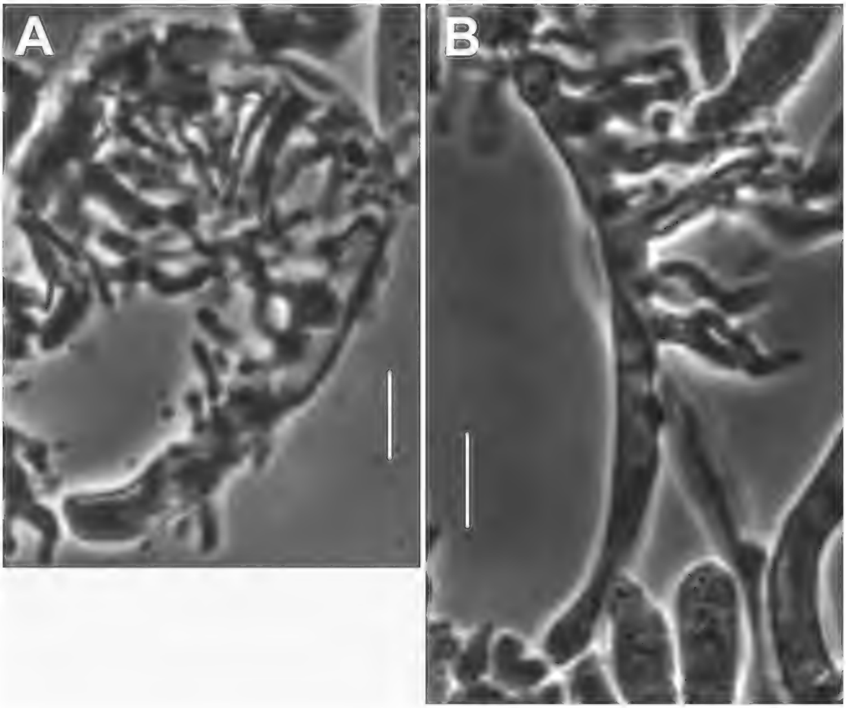


Fig. 22. *Collybiopsis filamentipes*. (TFB 13962; TENN-F-065861). Diverticulate hyphae of the hymenium. Scale bars = 10 µm.

and molecular evidence. That *Co. ramealis* seems not to occur in North America, and seems replaced by *Co. californica, Co. filamentipes* and *Co. furtiva* reflects the same situation in other agaric groups [e.g., *Megacollybia rodmanii* for *M. platyphylla* (Hughes & al. 2008); *Collybiopsis confluens* subsp. *campanulatus* in North America for the type subspecies in Europe (Hughes & Petersen 2015); *Sparassis americana* for *S. crispa* (Hughes & al. (2014, 2015)].

Interestingly, some years after collection of the holotype specimen in 2011, the Hesler specimen was discovered in the herbarium under "*Marasmiellus* sp.," collected some 40 years previously within 100 m from the topotype location.

Additional specimen examined: **USA, Tennessee, Knox Co.**, Knoxville, Timberlake Dr., Hesler's house, 1.VIII.1970, coll. LR Hesler, LRH 35861 (TENN-F-035861).

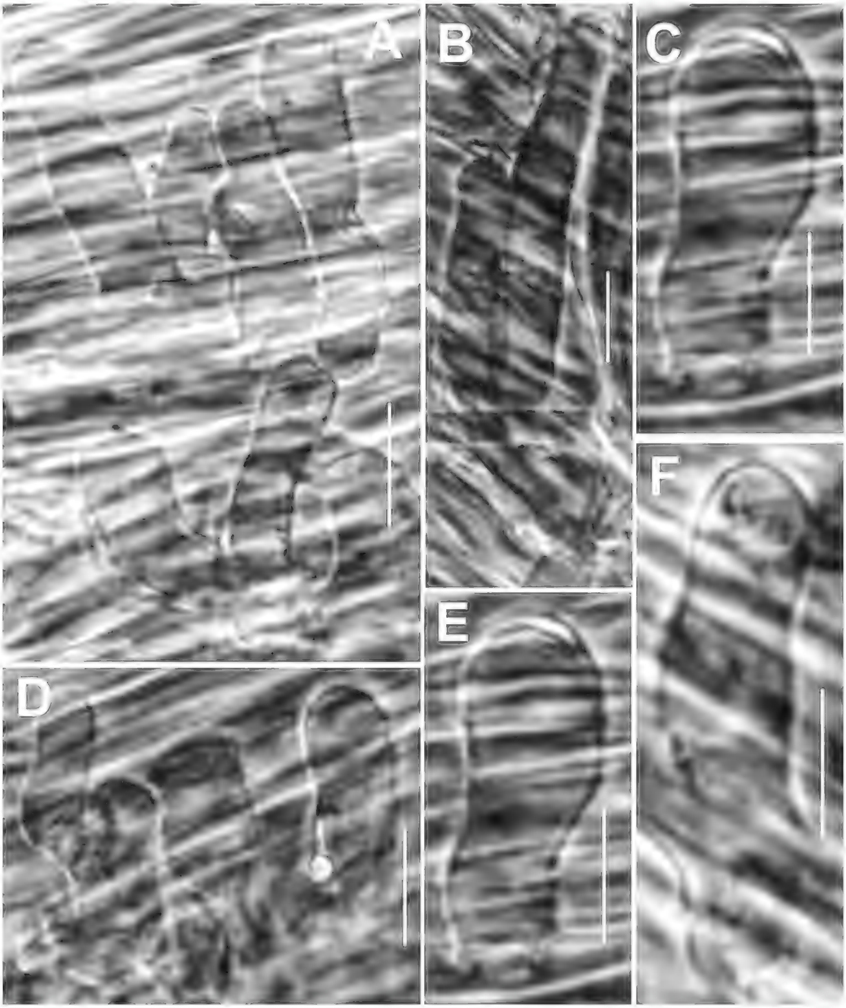


Fig. 23. *Collybiopsis filamentipes*. (TFB 13962; TENN-F-065861). Caulocystidia. A, B, D. Clusters of Caulocystidia. C, E, F. Individual caulocystidia. Scale bars = 10 µm.

Collybiopsis furtiva R.H. Petersen, **sp. nov.** Figs. 24-34

IF 556208

Differs from Old World *Co. ramealis* by its distinct molecular profile; its hyaline (not pigmented) cheilocystidia; and its generally smaller basidiomata.

Type: USA, North Carolina, Macon Co., vic. Highlands, Horse Cove, Rustic Falls area, 35°02′17″N 83°09′32″W, 10.VIII.1987, coll. DE Desjardin (as *Ma. ramealis*), DED 4425 (**Holotype**, SSFU-F-024540).

Etymology: *furtiva* = furtive, underhanded, secretive, referring to prior identification as *Co. ramealis.*

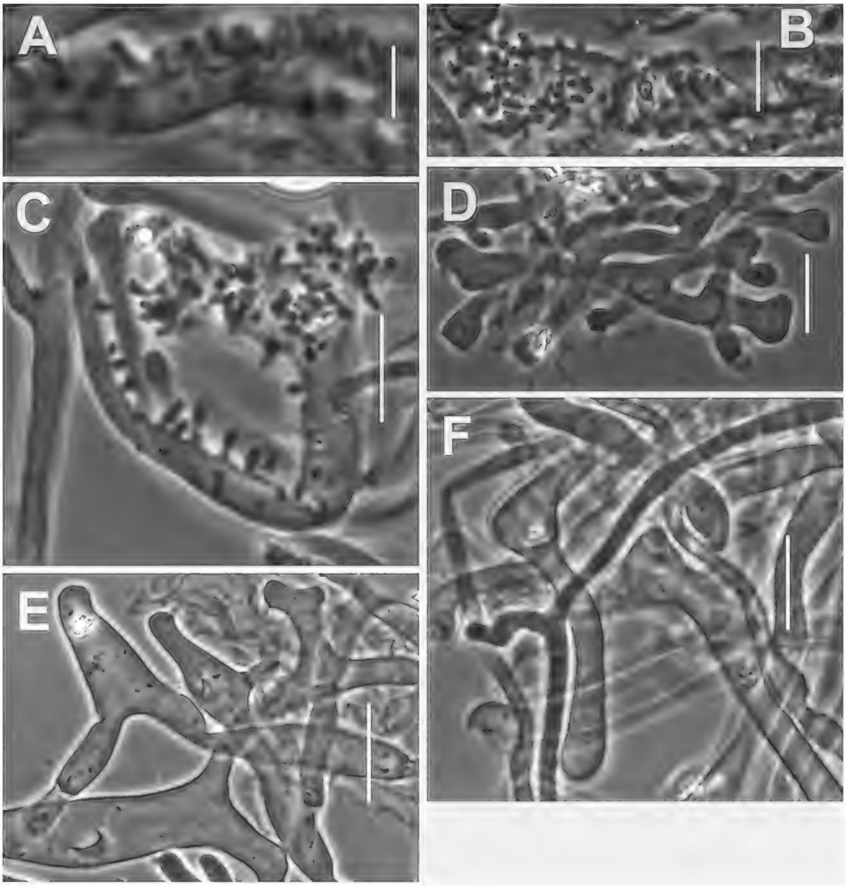


Fig. 24. *Collybiopsis furtiva.* (TFB 11558; TENN-F-059444). Pileipellis and pileus trama. A, B. Diverticulate hyphae of pileus surface. C. Diverticulate hypha ending in a "broom cell-like" hyphal terminus. D. "Antler-shaped" hyphae of subpellis. E. Swollen cells of pileus trama. F. Slender hypha among swollen hyphae of pileus trama. Scale bars = 10 µm.

Basidiomata diminutive, ratio of stipe length to pileus diameter low. Pileus 5–12 mm broad, strongly convex to subglobose when young, expanding to become shallowly convex to plano-convex with involute margin, finally applanate with upturned margin, opaque, consistently sulcate-striate near margin, matt; disc unicolorous or tinged brownish to avellaneous, otherwise white, orange-white, cream, pinkish cream, grayish-orange 5B2-3, pale orange white 6A2 developing necropigment near "ochraceous buff" 5A5. Lamellae adnexed to decurrent by a tooth, close to subdistant (L + ll = 35–52; L = 11–16), thickish, with little or no anastomosis but occasionally showing common forking near pileus margin in large basidiomata, becoming crisped in or after drying, seceding and then sometimes appearing pseudocollariate, white to cream white, near "pale olive buff" 3B2, or buff when fresh, developing

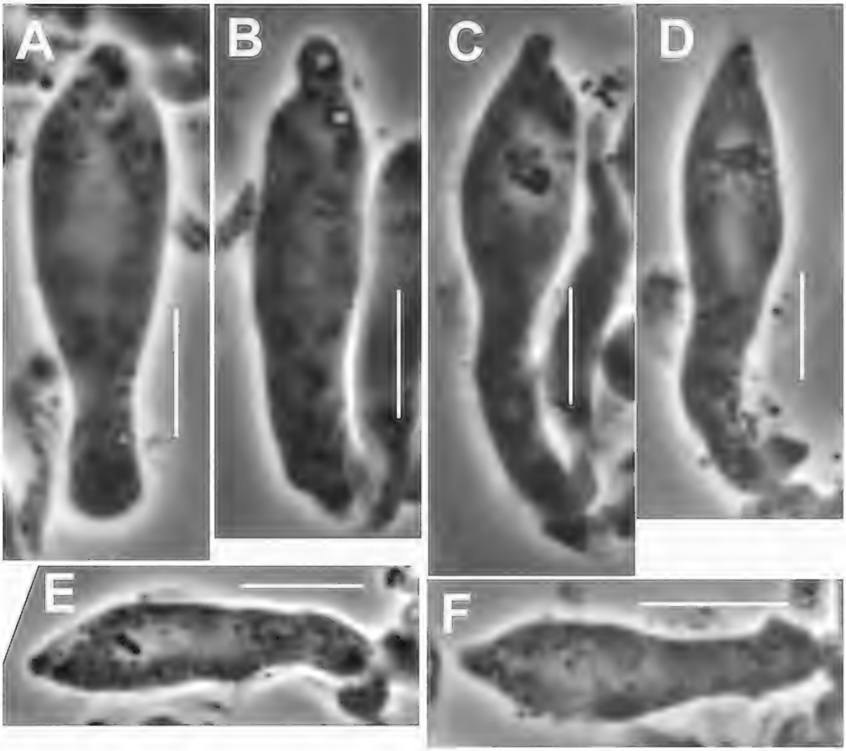


Fig. 25. *Collybiopsis furtiva*. (DED 4410; TENN-F-057309). Pleurocystidia. Note submammillate apices; clamp connection in E. Scale bars = 10 µm.

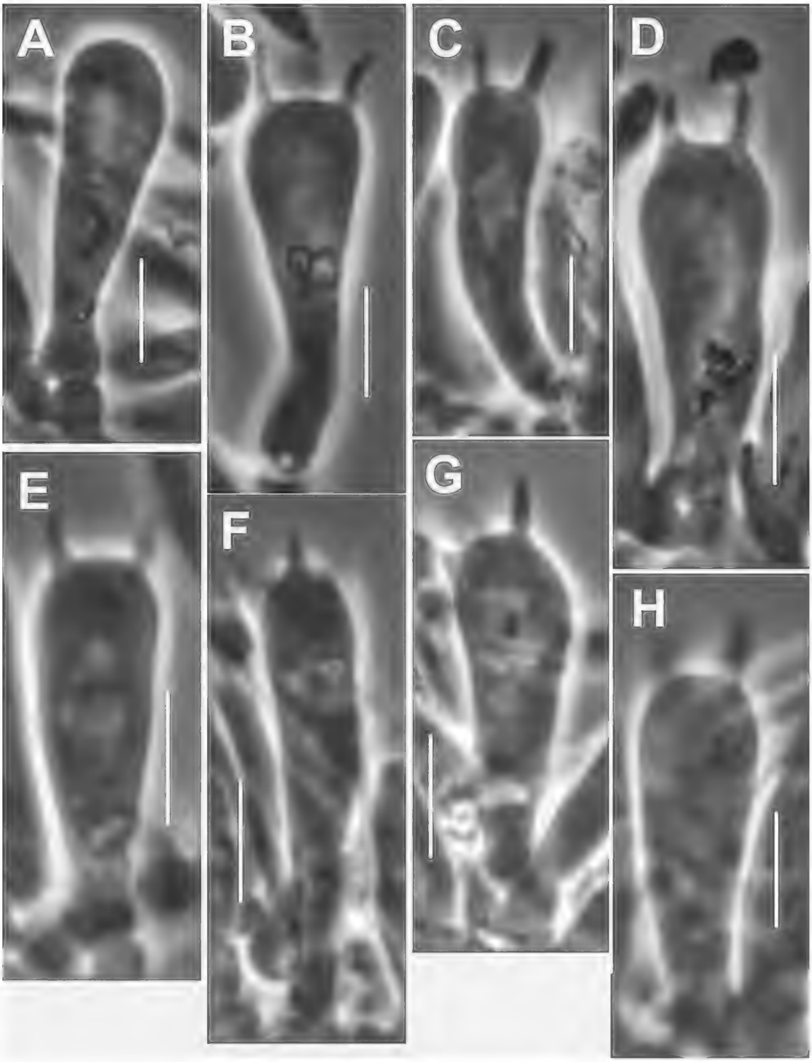


Fig. 26. *Collybiopsis furtiva*. (TFB 11550; TENN-F-059444). Basidioles and basidia. A. Basidiole. B-H. Mature basidia. Note clamp connections in A, D, F. Scale bars = 10 µm.

ruddy necropigment; lamellar edge fimbriate or appearing crystalline, eroded, remaining white to buff or "pale pinkish buff" 6A2, but not marginate when fresh. Stipe 4–11 × 0.3–1.2 mm, terete or somewhat compressed upward,

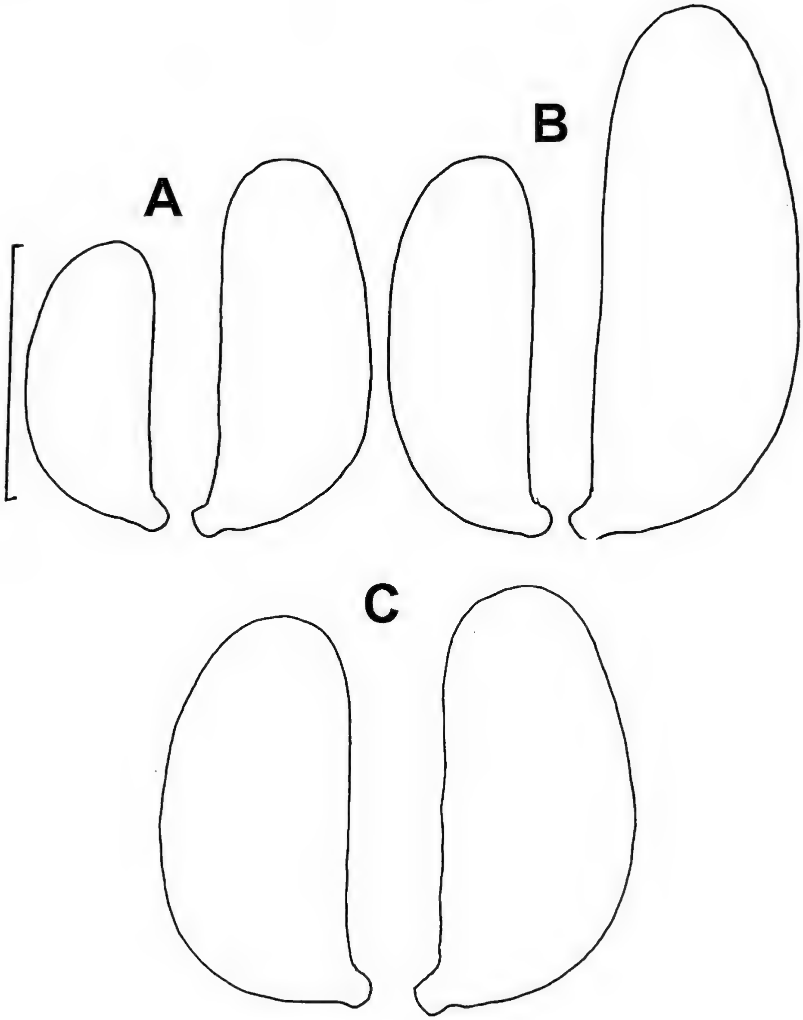


Fig. 27. Basidiospores of *Collybiopsis* taxa.
A. *Collybiopsis furtiva*. (DED 4410; TENN-F-057309).
B. *Collybiopsis furtiva*. (DED 3973; SFSU-F-024523).
C. *Collybiopsis minor*. (TFB 11930; TENN-F-059993).
Scale bars = 10 µm.

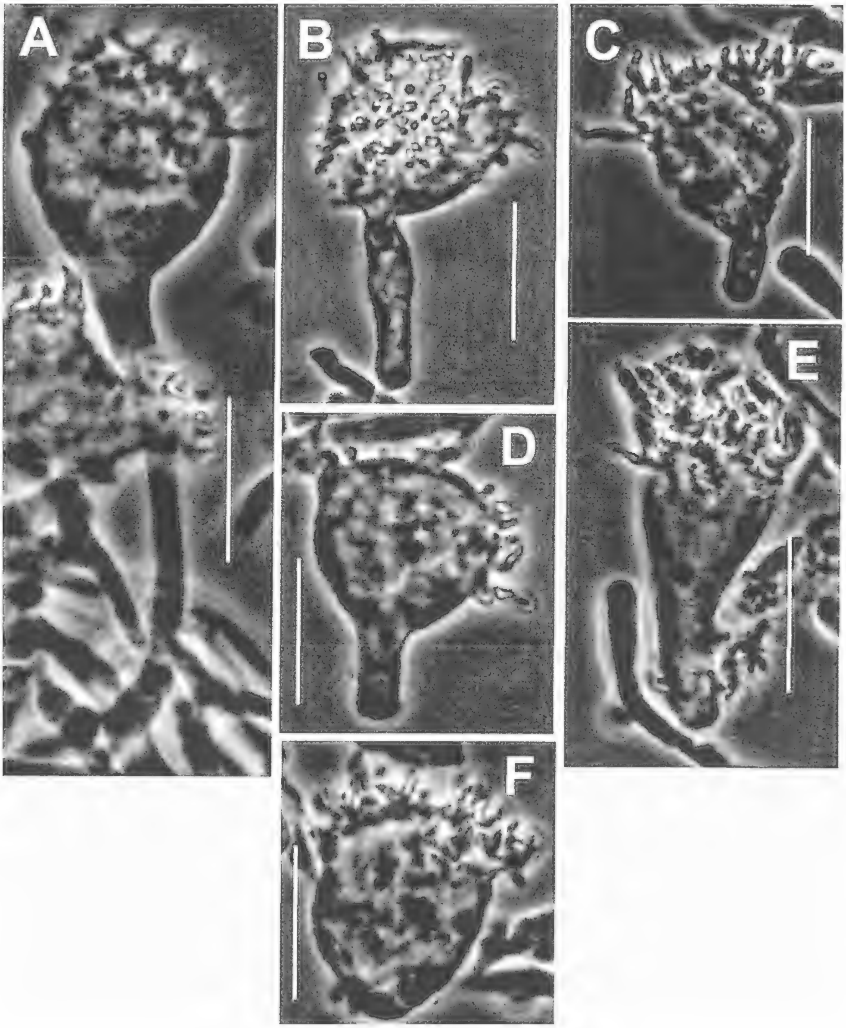


Fig. 28. *Collybiopsis furtiva*. (DED 4425; SFSU-F-024540). Cheilocystidia. Scale bars = 10 μm.

equal or tapered downward and then with minute snow white ring or ruff on stipe base, straight to curved (in drying?), sometimes abruptly pinched at base (similar to adult *Ma. praeacutus*), opaque or (now) appearing subcartilaginous, loosely stuffed to hollow; upper stipe appearing glabrous to minutely flocculose, concolorous with lamellae, not dextrinoid (sallow greenish yellow in IKI + BF);

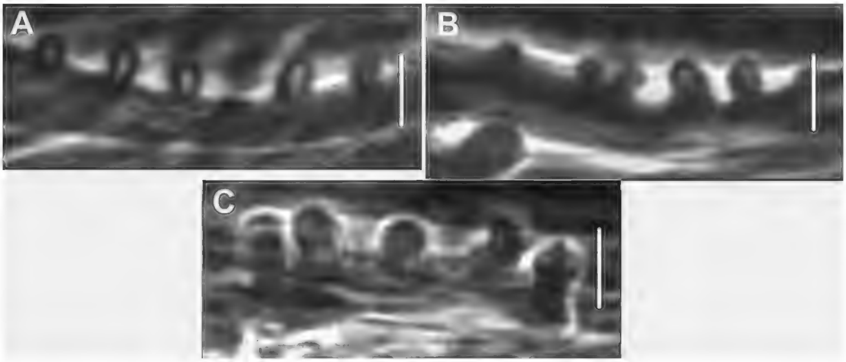


Fig. 29. *Collybiopsis furtiva*. (DED 4410; TENN-F-057309). Upper stipe surface.
Note files of simple lobate branches.
Scale bars = 10 µm

lower stipe (basal ~1/5) appearing flocculose to wispy, in age light brown 6D6, "avellaneous" 7B3, reddish brown black to slightly brownish orange 6C5-6when young; insertion appearing insititious. Odor negligible; taste negligible.

Habitat & phenology: Gregarious; fruiting on well-rotted wood and dead twigs of *Rhododendron maximum*, *Tsuga*, various hardwoods, rarely on bark of grape; eastern United States (common in southern Appalachian Mountains); mid-summer.

Pileipellis a well-developed *Rameales*-structure with two types of hyphae: 1) repent hyphae (Fig. 24A, B) 2.5–6.5 µm diam, beset with diverticula; diverticula 1–6.5(–9) × 1–2 µm, appearing stiff, nodulose to strangulate, often dichotomously branched, refringent (PhC); and 2) common hyphal termini (Fig. 24C) otherwise resembling the repent hyphae with similar diverticula. Subpellis including free-form or "antler-shaped" hyphal segments and termini (Fig. 24D-F). Pileus and lamellar tramae loosely interwoven, composed of three hyphal types: 1) hyphae 2.5–6.5(–14) µm diam, firm-walled, conspicuously clamped; 2) basically similar but with long, free-form, hyaline, inflated cells <15 µm diam; and 3) occasional slender hyphae with thickened walls and dense cytoplasm suggestive of gelatinization. Pleurocystidia (Fig. 25) abundant to often scattered, 20–35 × 6–9 µm, hyaline, fusiform, sharply attenuate distally and occasionally submammillate, conspicuously clamped; contents often vaguely partitioned at very apex. Basidioles (Fig. 26A) clavate; basidia (Fig. 26B–H) 20–28 × 6–7 µm, narrowly clavate, not capitulate, 4-sterigmate,

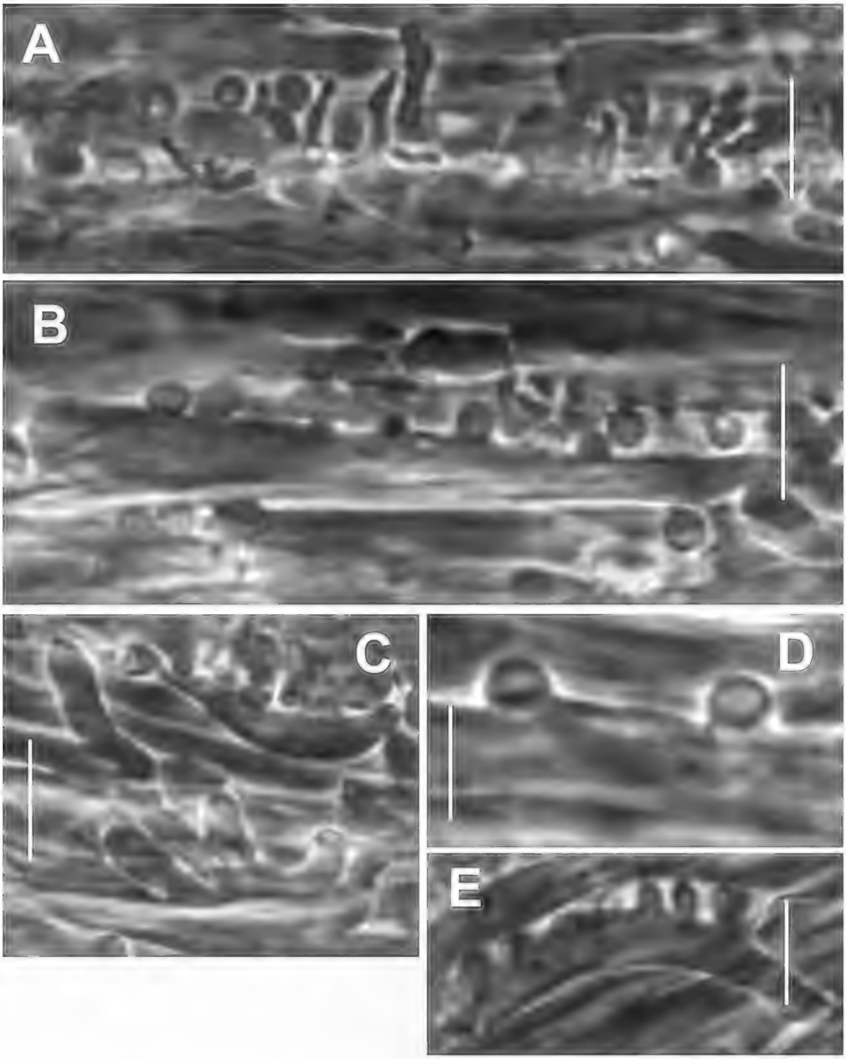


Fig. 30. *Collybiopsis furtiva.* (DED 4410; TENN-F-057309). Lower stipe surface. A, B, E. Files of surface lobate branches. D. Two lobate branches with suggestion of slime matrix. Scale bars = 10 µm.

conspicuously clamped. Basidiospores (Fig. 27A) (6–)6.5–9(–10) × 2.5–3(–3.5) µm ($E = 1.86–3.50$; $E^m = 2.75$; $L^m = 7.6$ µm), elongate-ellipsoid, tapered proximally (marasmioid), thin-walled, hyaline, inamyloid. Cheilocystidia

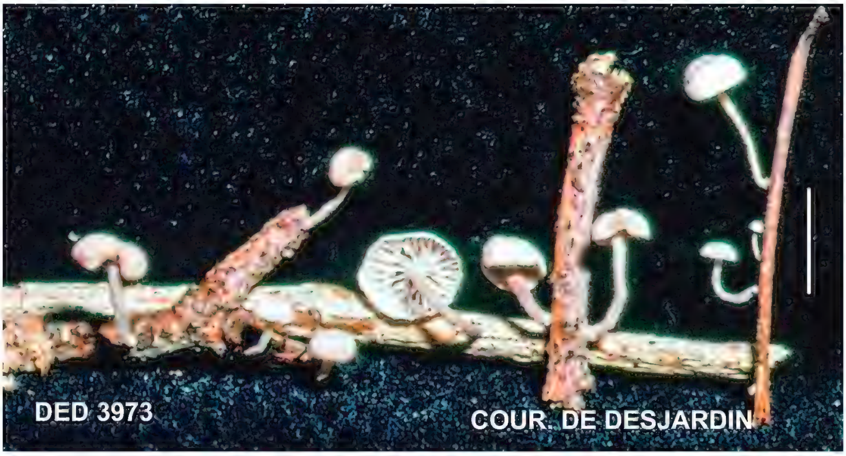


FIG. 31. *Collybiopsis furtiva*. (DED 3973; SFSU-F-024523). Basidiomata.
Scale bar = 10 mm. Photo courtesy of DE Desjardin.

(FIG. 28) hyaline, thin-walled, always obscurely clamped, very variable from clavate (<50 × 10–13 µm) with scattered diverticula over the apical 15–20 µm, shorter (base not seen), branched (branches 6-8 µm broad, variably diverticulate) to ventricose-rostrate, stalked (<50 µm long) with apical inflation <20 µm broad, smooth or beset with diverticula varying from papillate (*rotalis*-like) to tentacular (<10 × 1–1.5 µm). UPPER STIPE MEDULLA consistent with medulla of lower stipe (see below); upper stipe cortical hyphae also similar, but surface lobate branches (FIG. 29) seem consistently simple, knobby, not vermiform, perhaps thick-walled, subrefringent. LOWER STIPE MEDULLA in minimal slime matrix. Hyphae of two types: 1) broad, 4–7.5 µm diam., hyaline, thick-walled (wall <2.5 µm thick with evidence of individual gelatinization), obscurely clamped; and 2) slender, 1.5–3 µm diam., firm- to thick-walled, conspicuously clamped, occasionally with incomplete clamps (i.e., small, curved, hook-like branches). No tissue dextrinoid. Lower stipe cortical hyphae (FIG. 20) 3.5–7.5 µm diam, thick-walled, pigmented (ochraceous brown), producing small, thickly scattered, hyaline, thin-walled, nodulose to vermiform branches (caulocystidia; FIG. 29) 3.5–6.5 µm broad. CAULOCYSTIDIA of two types: 1) digitate or peg-like individuals (FIG. 30A, B, E) arising from cortical hyphae as side branches, 4–13 × 2.5–4 µm; and 2) cheilocystidia-like (FIG. 30D), with inflated portions surmounted by numerous lobe-like diverticula.

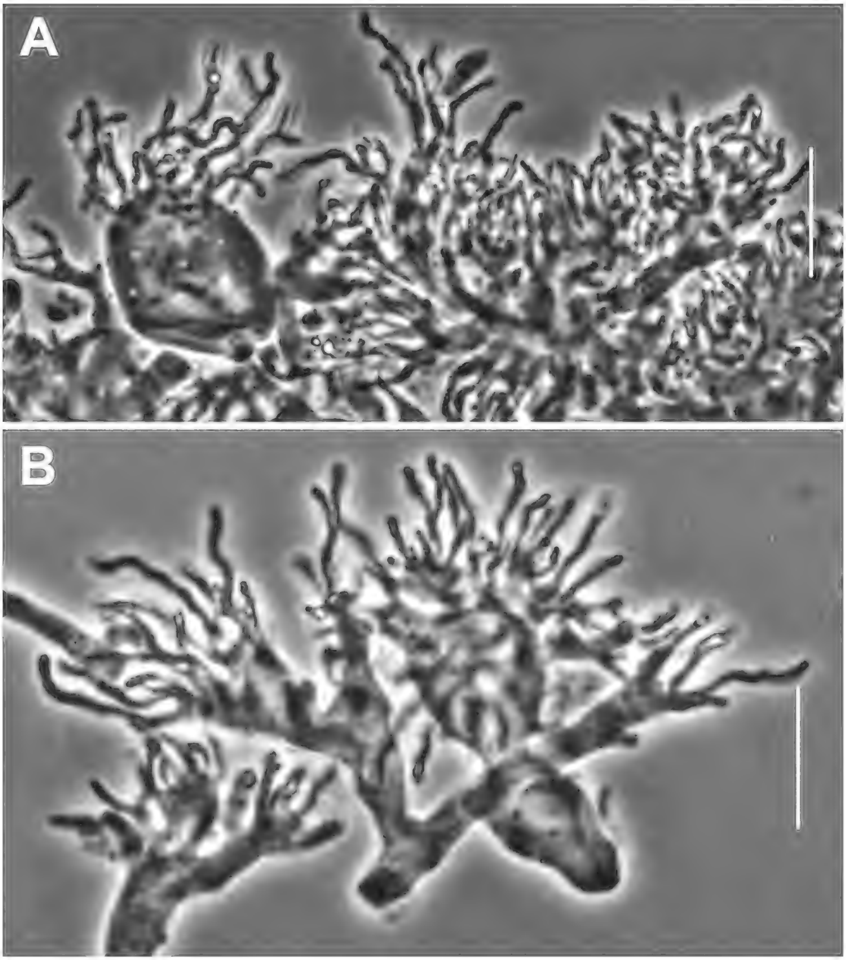


Fig. 32. *Collybiopsis furtiva*. (DED 3973; SFSU-F-024523). Cheilocystidia. A. Cluster of cheilocystidia. B. Clavate individual plus divaricately branched individual. Scale bars = 10 µm.

Commentary: Most synonyms listed under *Agaricus ramealis* in Index Fungorum are homotypic (i.e., based on Bulliard's basionym). The European neotype designated by Antonín & Noordeloos (1993; France, Calais, Boulogne, Noordeloos 7310, L) serves to establish the taxonomic basis of these homotypic synonyms. Although numerous subspecies and varieties have been proposed, none have been explicitly based on North American material.

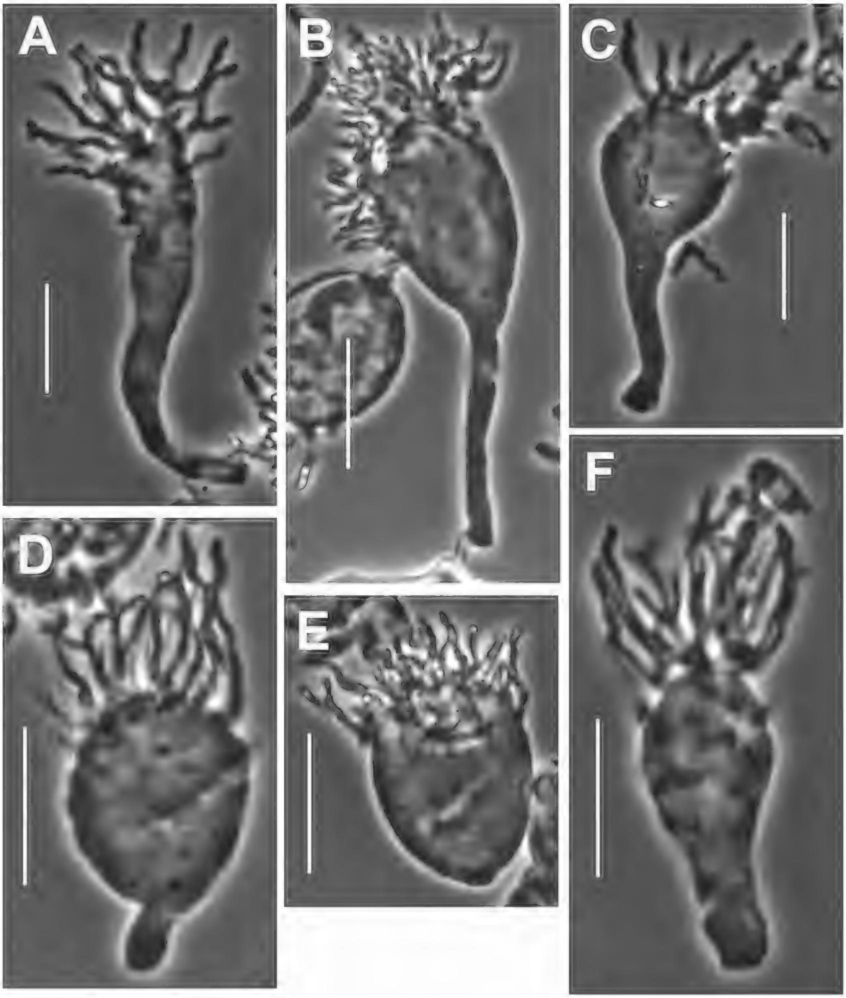


Fig. 33. *Collybiopsis furtiva*. (DED 3972; SFSU-F-024523). Ventricose-rostrate cheilocystidia. Note prominent diverticula. Scale bars = 10 µm.

In order to reach *Marasmiellus ramealis* in Desjardin's (1997) key to the genus in the southern Appalachian Mountains, the following characters are required (some a poor match to the description above): 1) basidiospores <10.5 µm long; 2) stipe central, habit marasmioid, collybioid or mycenoid, basidiomata NOT pleurotoid, not on monocots; 3) stipe base NOT attenuated to a narrow point, odor not alliaceous nor fetid; 4) pileipellis a well-developed *Rameales*-structure; 5) pileus pigmented overall (including pinkish brown); 6) rhizomorphs absent; 7) pileipellis lacking inflated terminal cells; 8) pileus yellowish brown vs dark brown to brown (separating from *Ma. nodosus*); 9) context <1 mm thick (vs. context 2–4 mm thick); 10) stipe 0.2–1 mm diam. (vs. stipe 2–3(–11) mm diam.; 11) basidiospores 2.5–4.5 µm broad (vs 4.5–7 µm broad); 12) cheilocystidia broadly clavate with numerous fine diverticula (vs cheilocystidia irregular in outline, often contorted, and with nodulose outgrowths); and 13) basidiomata formed on epigeous branches and stems of deciduous trees, shrubs or herbaceous dicots (vs basidiomata formed on hypogeous sticks or roots). According to Desjardin (1997), southeastern North America *M. ramealis* is most commonly confused with *Marasmius* (now *Mycetinis*) *opacus* with larger basidiomata and plentiful white rhizomorphs and rather different pileipellis (see Petersen & Hughes 2017b). Our observations indicate also a resemblance to *Ma. praeacutus*, distinguished in the field by its pinched stipe and common, persistent basidiomatal primordia.

Stipe surface ornamentation, especially upper stipe, comprises scattered lobes or nodes, more complex on lower stipe. When simple, such nodules are subrefringent, identical with diverticula of cheilocystidia and especially pileipellis *Rameales*-structure.

Parenthetically, it is interesting to know Earle's taxonomic concept of *Marasmius ramealis*. Specimen Earle 767 (collected on N.Y. Botanical Garden grounds and identified by Earle; NY) may be representative. Although microscopic structures are collapsed, diagnostic characters do not totally agree with those of eastern North American *Co. "ramealis"* (see above). No attempt has been made to extract DNA.

We need to note here an abnormal collection of *Co. furtiva* (DED 3973, SFSU-F-024523 as *Ma. ramealis*), collected in the same general area as several other species. Significantly, its nrITS sequence does not differ from those of several other *Co. furtiva* collections, yet the basidiomata (Fig. 31) are anatomically distinct, particularly the cheilocystidia and stipe ornamentation. In DED 3973 cheilocystidia (Figs. 32, 33) 45–60 × 9–19 µm (at widest point), appear to arise deep in the hymenophoral trama (surely longer than basidia or pleurocystidia); are ventricose-rostrate, stalked with an inflated terminus, and rarely branched; and include scattered small, broadly clavate individuals; the stalks (25–40 × 3–5.5 µm) are conspicuously clamped, thin-walled, easily distorted or disarticulated with termini that are inflated, thin-walled, unpigmented, and beset with

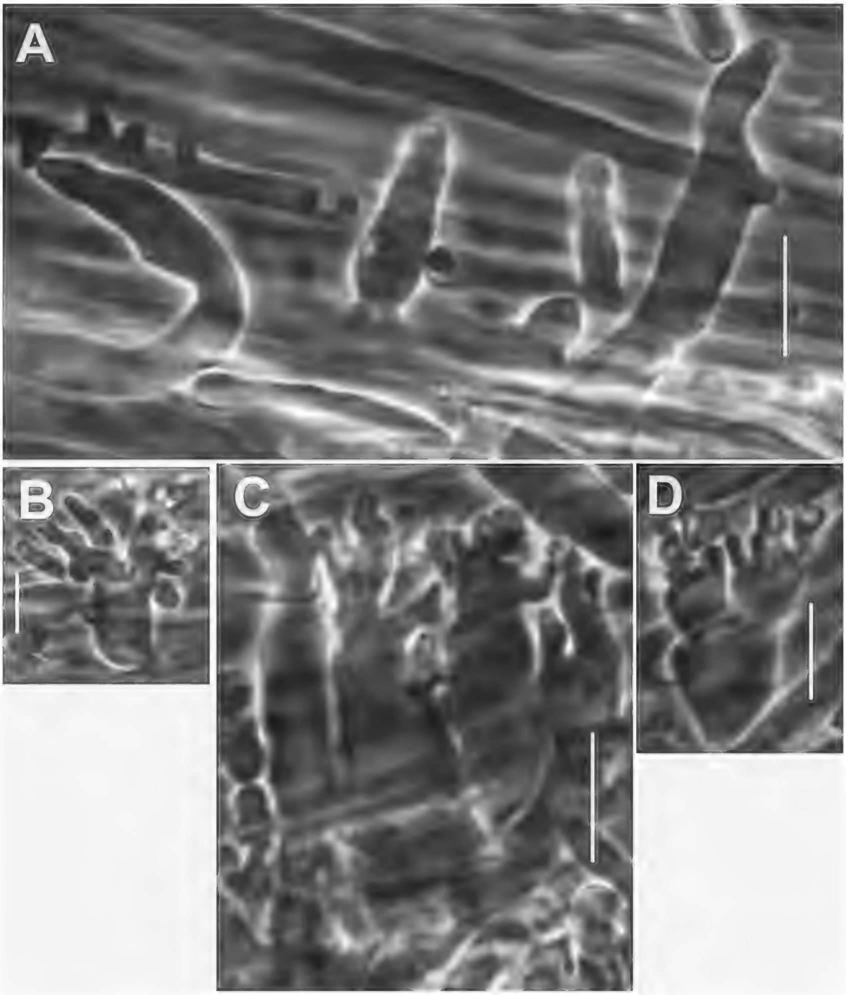


Fig. 34. *Collybiopsis furtiva.* (DED 3973; SFSU-F-024523). Caulocystidial structures. A. Individual caulocystidia. B-D. Coralloid, cheilocystidial structures. Scale bars = 10 µm.

numerous (<70) medusoid diverticula; the slender long diverticula (<25 × 1–1.5 µm) are usually elongate-digitate but occasionally dichotomously branched, gnarled, subnodulose, and often apically refringent (PhC). Basidiospores (Fig. 27) are significantly larger than those of *Co. furtiva.* The stipe ornamentation consists of both individual hyphal caulocystidia and coralloid cheilocystidial structures; individual hyphal caulocystidia

(Fig. 34A) 6–75 × 5–9 µm, thick-walled (wall <2 µm thick, pallid greenish ochraceous PhC), sometimes appearing in "picket fence" files, broadly rounded to setoid with sharply acute apex; caulocystidia resembling cheilocystidia (Fig. 34B-D) 15–45 × 9–15 µm, coralloid with peg-like or capitulate diverticula, thick-walled (wall <1 µm, hyaline). Lower stipe ornamented with accumulated heaps of mixed caulocystidial structures.

Probably coincidentally, the submammillate pleurocystidial apices of *Co. furtiva* resemble those of an unidentified *Collybiopsis* (TFB 23217; TENN-F-023217) close to *Gymnopus subnudus* in *G.* sect. *Vestipedes* (Fig. 1).

Cheilocystidia of DED 3973 resemble those of *Co. californica* (q.v.) but our molecular nrITS phylogeny (Fig. 2) places its sequence with other southeastern collections typical of *Co. furtiva.* Coralloid cheilocystidial stipe vesture elements seem unique.

Additional specimens examined: **USA, Georgia, Rabun Co.**, vic. Clayton, Warwoman Dell Picnic Area, 34°52′58″N 83°20′58″W, 6/15/1992, coll. SA Gordon, TFB 4796 (TENN-F-051097). **New York, Bronx Co.**, "Bronx Woods," det. WA Murrill, VIII.1911 (02755903 NY). **North Carolina, Macon Co.**, vic. Highlands, Bull Pen Rd., 28.VII.1987. coll. TJ Baroni, det. DE Desjardin, DED 4410 (TENN-F-057309); vic. Highlands, Horse Cove, Rustic Falls area, 12.VII.1984, coll. & det. DE Desjardin, DED 4584 (SFSU-F-024508); vic. Highlands, Cliffside Lake Campground, 29.VII.1986, coll. & det. DE Desjardin, DED 3973 (SFSU-F-024523); 35°02′24″N 83°27′12″W, 30.VI.2002, coll. RHP, TFB 11558 (TENN-F-059444); vic. Otto, Coweeta Hydrologic Laboratory, Ball Creek Rd., 26.VI.1993, coll. & det. DE Desjardin, DED 5796 (SFSU-F-024524). **Tennessee, Blount Co.**, GSMNP, Cades Cove, 35°35′39″N 83°50′31″W, 15.VI.1957, coll LR Hesler, TFB 7867 (TENN-F-007867).

Collybiopsis hasanskyensis R.H. Petersen, **sp. nov.** Figs. 35-41

IF 557072

Differs from other *Collybiopsis* taxa by its diminutive basidiomata that fruit on *Alnus* twigs and strobili; its unique ITS sequence; its gymnopoid pileipellis lacking a *Rameales*-structure; its stalked-clavate, smooth to lobate to diverticulate cheilocystidia that are larger than basidia and pleurocystidia, and its pale buff necropigment.

Type: Russia, Primorsky krai, Hasansky Dist., vic. Primorsky, Kedrovaya Reserve, 43°05.87′N 131°33.57′E, 18.VIII.2005, coll RHP, A. Kovalenko, TFB 11846 (Holotype, TENN-F-060730).

Etymology: Hasansky; district in Primorsky Region of Russia, where the holotype was collected.

Basidiomata (Fig. 31A) diminutive. Pileus 4–8 mm broad, plane to somewhat depressed with involute margin, matt, delicately radially wrinkled, inward "pinkish buff" 6A3, outward "pale cinnamon pink" 5A2, becoming

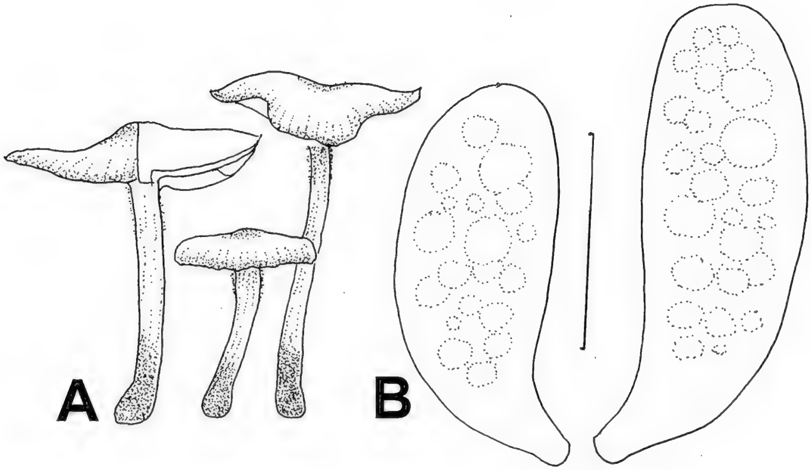


Fig. 35. *Collybiopsis hasanskyensis*. (TFB 11846; TENN-F-060730).
A. Basidiomata B. Basidiospores Scale bar: A = 5 mm; B = 5 µm.

off-white with pale cantaloupe-colored necropigment; pileus context thin, brittle when dried, white. Hymenophore developing a pallid cantaloupe necropigment. Lamellae adnate to shallowly decurrent, subdistant to distant, varying from knife-like and then occasionally ventricose (<0.5 mm broad), to reduced to thin pleats, rarely with dichotomy but often buttressed or cross-veined, color unchanged from fresh (off-white with pinkish tint), L + ll = (22–)36–40, L = (9–)12–16, off-white with pinkish tint. Stipe 6–9 × 0.6–0.8 mm, equal to tapering somewhat upward, sometimes with base slightly enlarged to club-shaped, inserted only at base of club, apically minutely roughened (60×), soon appearing glabrous, now cartilaginous (glabrous-shining), pale apically, "sayal brown" 6C5 to dirty grayish brown downward, developing rich cantaloupe necropigment uniformly, consistently with small, off-white, circular, appressed basal pad. Odor and taste negligible. Rhizomorphs not observed.

Habitat & distribution: Fruiting on dead *Alnus* twigs and strobili; late summer and early autumn; presently known only from Hasansky District of far-eastern Russia near North Korea.

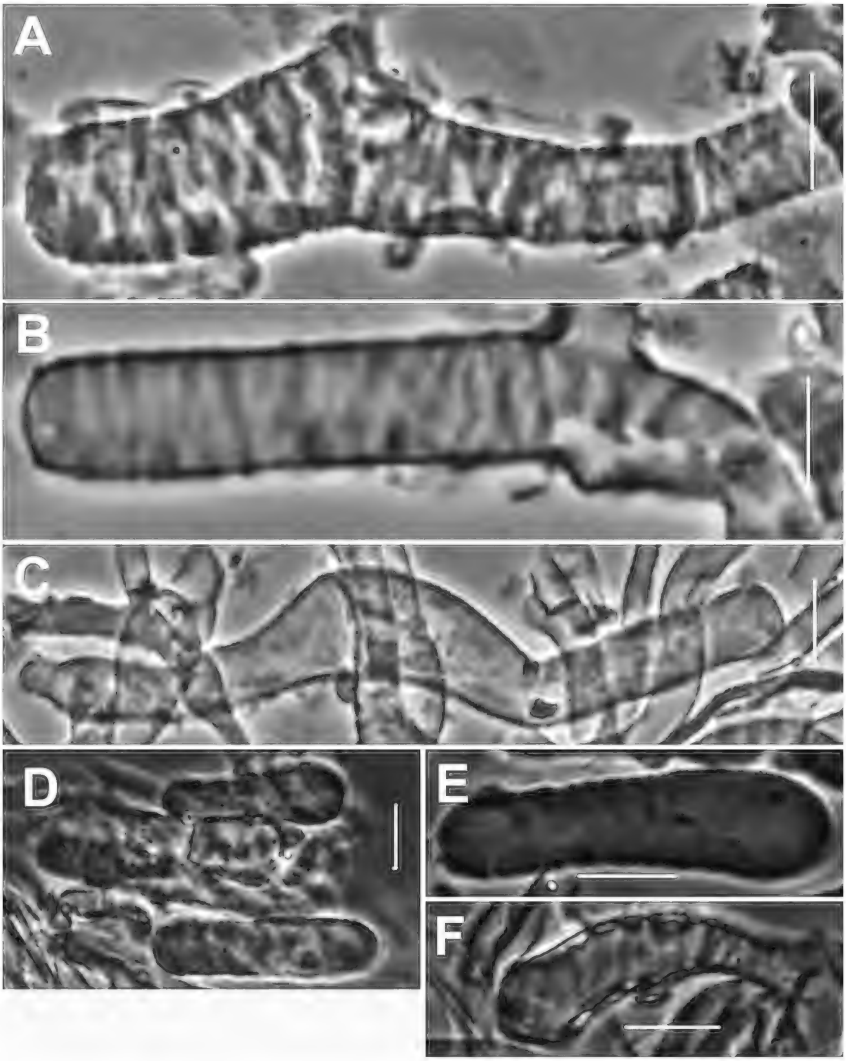


Fig. 36. *Collybiopsis hasanskyensis*. (TFB 11846; TENN-F-060730). Pileipellis hyphae. A. Heavy annular ornamentation. B. Weak annular ornamentation. C. Hypha with dense contents. D, E. Roughened, "cigar-shaped" hyphal segments. F. Thick-walled hypha with substantial profile calluses. Scale bar 10 µm.

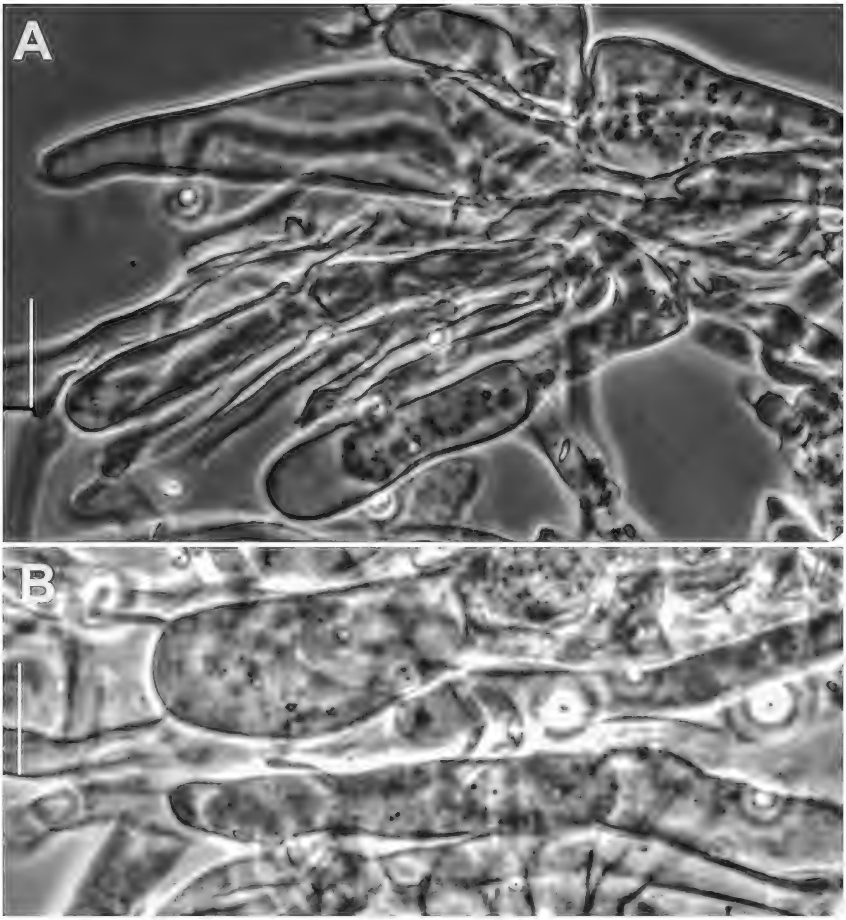


Fig. 37. *Collybiopsis hasanskyensis.* (TFB 11846; TENN-F-060730). Lamellar trama. A. Trama, showing inflated hyphae. B. Hyphal fragments with dense contents. Scale bar = 10 µm.

Pileipellis a repent layer of hyphae 4.5–13 µm diam, of several types: 1) thin-walled, without ornamentation, conspicuously clamped; 2) firm- to thick-walled (wall <1 µm thick, hyaline), ornamented (Fig. 36C) with two types of thickening; a) hardly visible in profile but vaguely annular in face view (Fig. 36B); b) prominent in profile view with conspicuous profile calluses (Fig. 36F); profile calluses <1.5 µm thick, lens-shaped, hyaline, refringent, conspicuously clamped; 3) disarticulated, somewhat inflated cells, cylindrical or cigar-shaped, thick-walled (wall <1 µm thick),

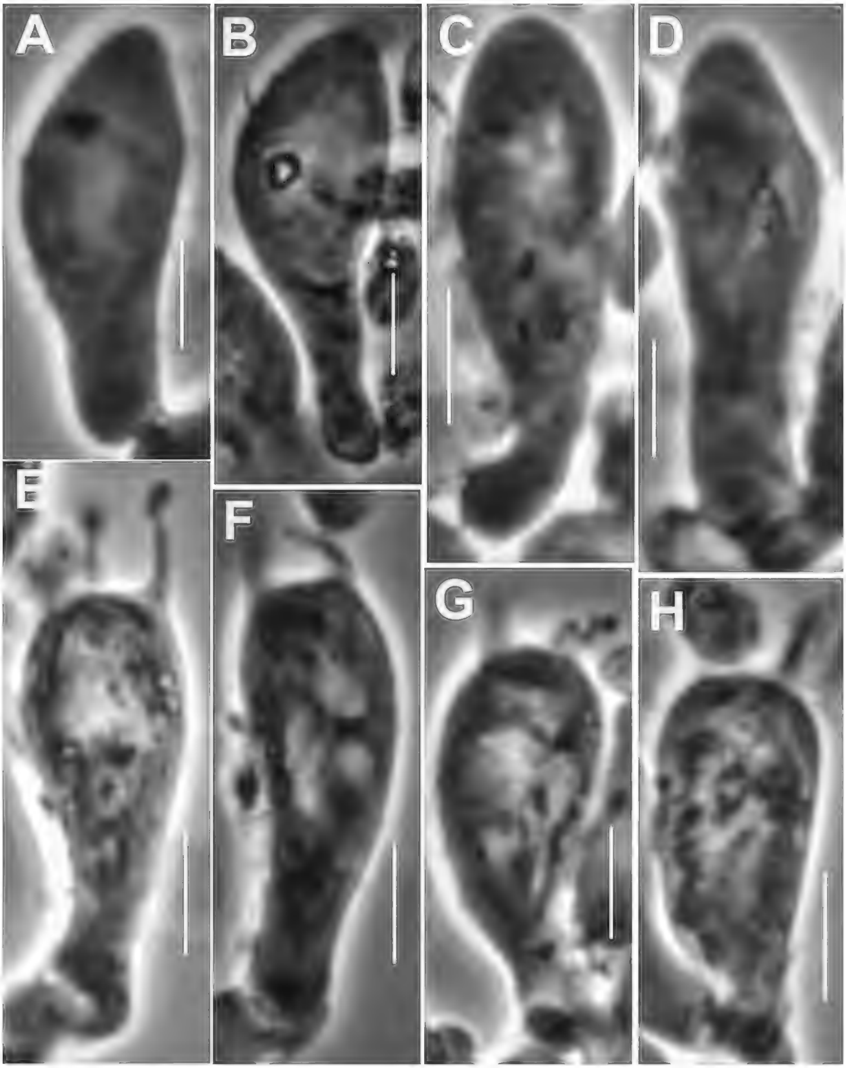


Fig. 38. *Collybiopsis hasanskyensis*. (TFB 11846; TENN-F-060730). Hymenial structures. A-D. Pleurocystidia. E-H. Basidia. Note clamp connection in E. Scale bar = 10 µm.

delicately ornamented in gregarious plaques (Fig. 36D, E); and 4) repent, thin-walled hyphae 4–8 µm diam, heavily ornamented with pigmented plaques, perhaps crystalline, protruding from the hyphal wall angularly <4 µm high (Fig. 36A). Note: no evidence of *Rameales*-structure. Pileus and

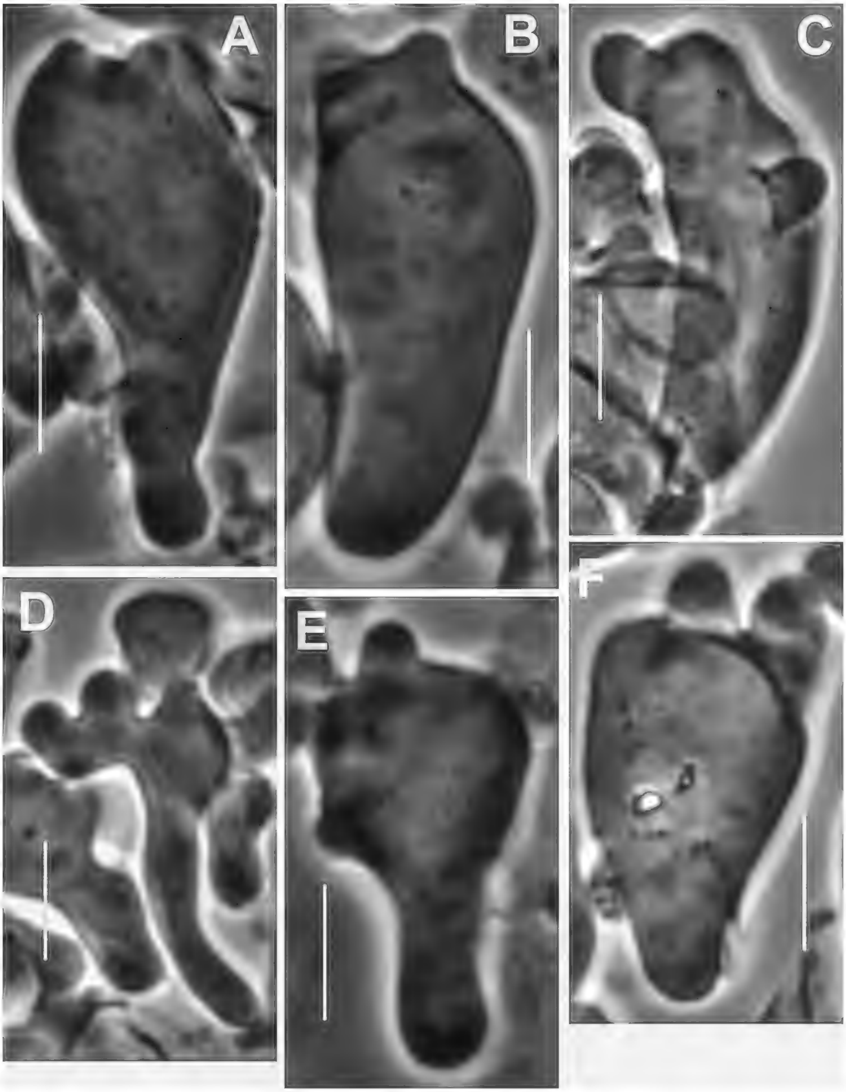


FIG. 39. *Collybiopsis hasanskyensis.* (TFB 11846; TENN-F-060730).
Typical cheilocystidia. Scale bars = 10 µm.

lamellar trama interwoven (FIG. 37), more tightly so under hymenophore; hyphae 3–6.5(–14) µm diam, firm-walled, hyaline, without slime sheath or matrix, conspicuously clamped. Subhymenial hyphae seem to disintegrate

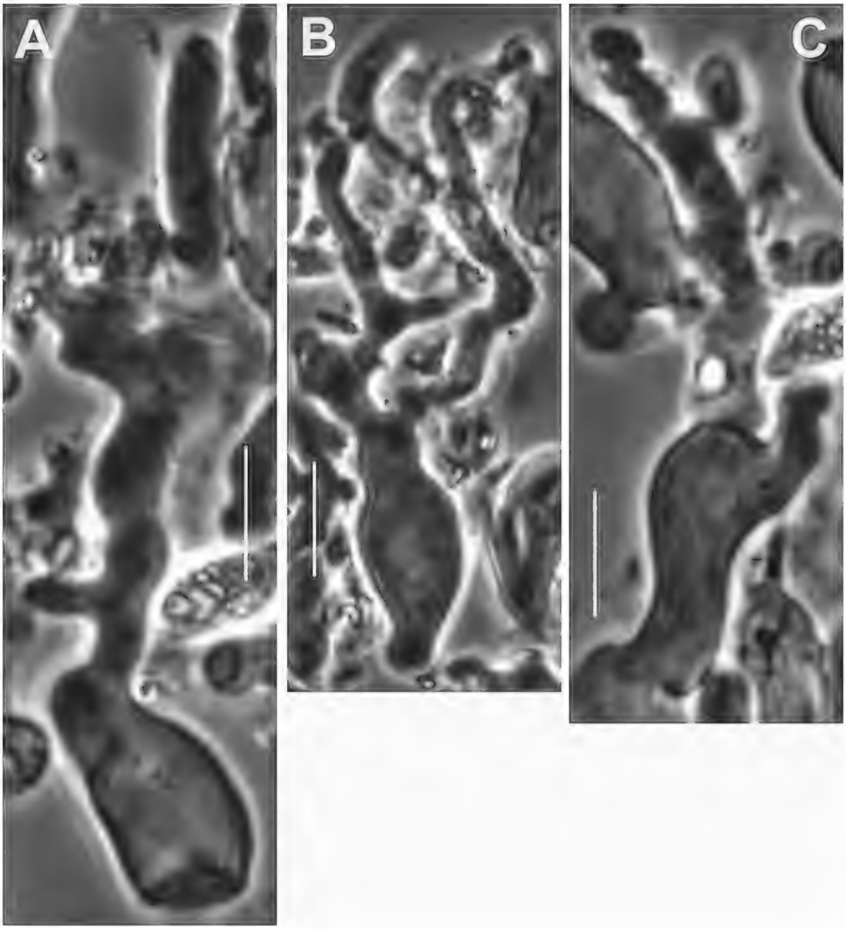


Fig. 40. *Collybiopsis hasanskyensis*. (TFB 11846; TENN-F-060730). Diverticulate cheilocystidia. Scale bars = 10 µm.

into debris, persistent after hymenial discharge making observation of basal clamps in the hymenium difficult. Evidence of gelatinization absent. Pleurocystidia (Fig. 38A–D) common, not abundant, stalked-fusiform, 19–22 × 9–11 µm at widest point, inconspicuously clamped; contents more or less homogeneous, not partitioned. Basidia (Fig. 38-H) digitate to clavate but not subcapitulate, 18–23 × 9–11 µm, occasionally suburniform, 2–4-sterigmate, inconspicuously clamped; sterigmata slender, lyre-shaped;

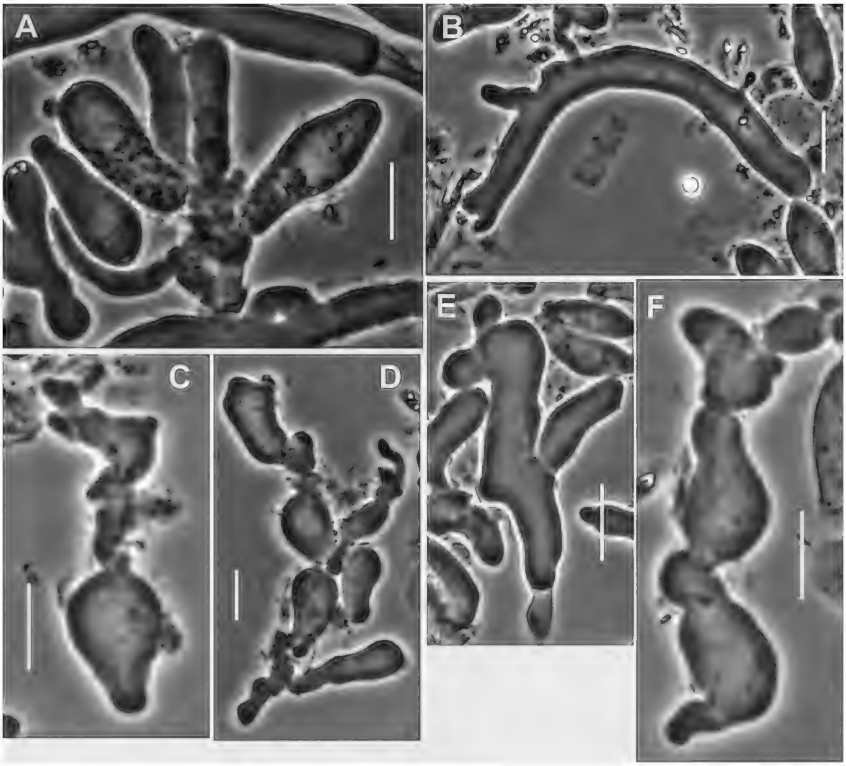


FIG. 41. *Collybiopsis hasanskyensis.* (TFB 11846; TENN-F-060730).
Caulocystidia. Scale bars = 10 µm.

contents heterogeneous, multi-granular with amorphous inclusions. BASIDIOSPORES (FIG. 35B) 7–11 × 3.5–4.5(–5.5) µm ($E = 1.82–2.75$; $E^m = 2.29$; $L^m = 8.8$ µm), elongate-ellipsoid, widely rounded distally, tapered proximally (marasmioid), thin-walled, hyaline, inamyloid; contents heterogeneous, foamy (i.e. multiguttulate). CHEILOCYSTIDIA (FIG. 39) abundant at lamellar edge, apparently easily disarticulated from basal septum (i.e., appearing without parent hyphae and with no evidence of clamp connection), firm- to thick-walled (wall <1 µm thick, hyaline, usually on emergent portion, not portions juxtaposed to other hymenial elements), very variable in shape from subglobose and without lobes, broadly clavate with expanded distal portion with one or few lobes, to columnar, to stalked with distal portion moderately expanded by with almost equal lobes, to occasionally grown out distally to form stout diverticula (FIG. 40); diverticula ≤40 × 3–5 µm, often lobed and occasionally branched; measurements really only approximate because forms are so variable, 30–42(–60) × 7–11 µm (at widest point), hyaline, often appearing empty (see photos). STIPE ANATOMY: no apparent differentiation of medullary versus cortical hyphae, all 4–6 µm diam, firm-walled (not thick-walled), obscurely clamped, apparently uniformly dextrinoid (cut ends of medullary hyphae just as dextrinoid as corticals); clamp connections, if present, inconspicuous. Stipe surface possibly with very thin slime matrix. Stipe apex with covering of inflated, free-form caulocystidia similar to inflated and distorted pleurocystidia (normal pleurocystidia and cheilocystidia common in this caulocystidial covering, some with tentacular apical outgrowths). CAULOCYSTIDIA (FIG. 41) (15–)20–40(–55) × (3-tentacular outgrowth) 8–14 µm, simple inflated utriform structures with almost invisible pedicel to repeatedly constricted "chains," occasionally a combination of tentacular and constricted structures. Lower stipe glabrous.

COMMENTARY: Although *Collybiopsis ramealis* exhibits a typical *Rameales*-structure pileipellis (as the archetype of the structure), this construction is not universal even in the *Co. ramealis* complex. Singer (1973) included nearly 20 Latin American taxa in *M.* subsect. *Ramealini*, but several did not exhibit the characteristic setulose repent hyphae and broom cell-like hyphal termini, and some were described as having a trichodermium of "thorny" or setulose hyphae. [*Marasmiellus foliiphilus* Dutta & al. (2015) was described and illustrated with such a trichodermium.] Likewise, *Co. hasanskyensis* lacks *Rameales*-structure in the pileipellis, instead showing typical gymnopoid repent hyphae, often with annular ornamentation.

FIG. 1 (ITS + LSU-based phylogeny) places *Co. hasanskyensis* sister to *Co. vaillantii* in the larger clade including *Co. eneficola* and *Co. biformis*.

ADDITIONAL SPECIMEN EXAMINED: **RUSSIA, PRIMORSKI KRAI, Hasansky Dist.**, vic. Primorsky, Kedrovaya Reserve, 43°05.87′N 131°33.57′E, 18.VIII.2005, coll. RHP, TFB 11847 (TENN-F-60731).

Collybiopsis minor R.H. Petersen, **sp. nov.** FIGS. 42-49

IF 556206

Differs from other *Collybiopsis* taxa by its habit on dead *Tsuga* twigs; its unique ITS rDNA molecular sequences; its pileipellis a repent layer of interwoven, non-diverticulate hyphae, often encrusted with annular deposit; its complete absence of gelatinized tissue; its pallid vestured stipe; and its conspicuously clamped hyphae (including hymenophore elements).

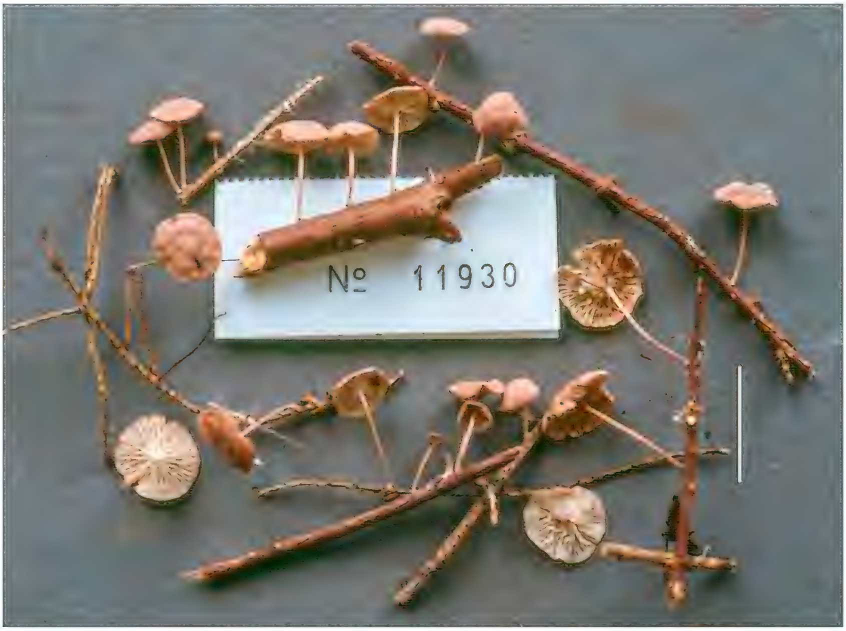


Fig. 42. *Collybiopsis minor*. (TFB 11930; TENN-F-059993). Dried basidiomata on *Tsuga* twigs. Scale bar = 10 mm.

Type: USA, Tennessee, Blount Co., GSMNP, Turkey Pen Ridge trailhead, 35°36′47″N 83°43′37″W 18.VI. 2004, coll. RHP, TFB 11930 (**Holotype**, TENN-F-059993).

Etymology: *Minor* = small, referring to the size of basidiomata.

Basidiomata (Fig. 41) diminutive. Pileus 4-9 mm broad, applanate, usually with down-curved margin, occasionally with shallow umbo, matt; disc and inner limb "army brown" 8D5 to "wood brown" 7C4; outer limb and margin "vinaceous buff" 9B2 to "tilleul buff" 7B2 (in drying remaining not far from "avellaneous" 7B3), not at all sulcate-striate; margin irregular as though eroded. Lamellae close (L + ll = 60-68; L = 20-24), adnexed (but without pseudocollarium), thin, subventricose (<1 mm broad), off-white when fresh, drying pallid yellowish with no necropigment; edges entire, somewhat paler than face; lamellulae in 2–3 ranks, plentiful at pileus margin. Stipe 8–15 × 1–1.5 mm, concolorous with pileus (more or less "avellaneous" 7B3) to somewhat more pallid or off-white where vestured, terete, equal or slightly tapering upward (base thicker than apex), lightly stuffed, vestured throughout; stipe base with conspicuous white ruff <0.5 mm high; insertion

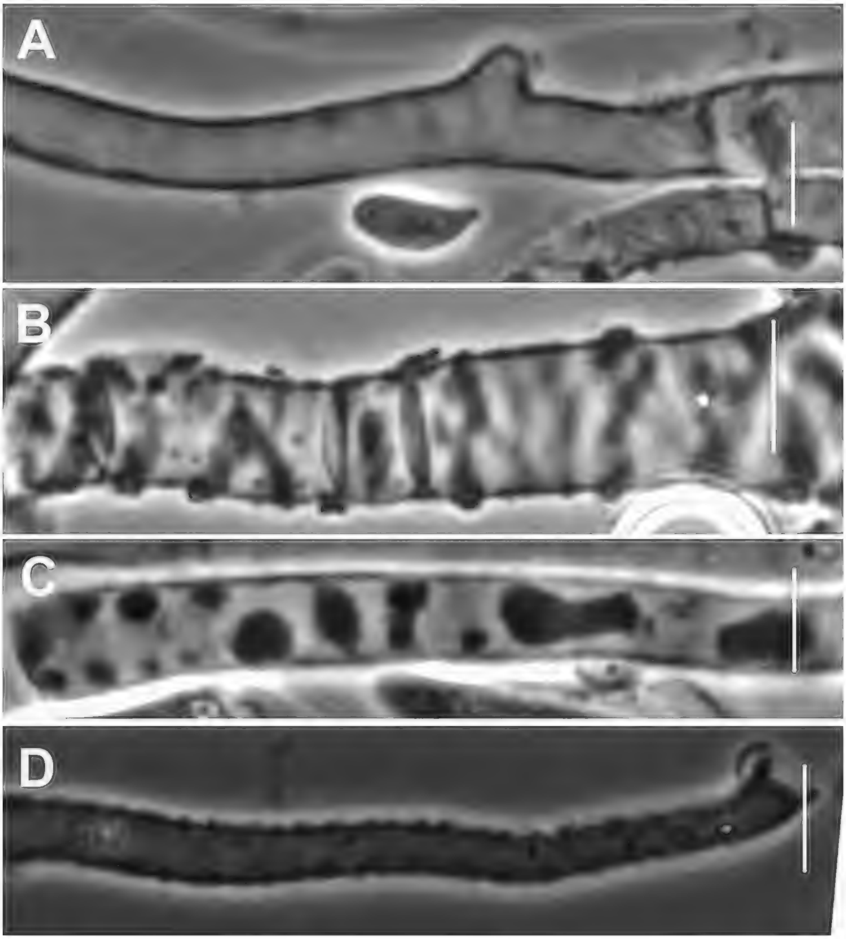


Fig. 43. *Collybiopsis minor*. (TFB 11930; TENN-F-059993). Pileipellis elements. A. Smooth, repent hyphae (note basidiospore); B. Hyphae with annular ornamentation; C. Hypha with contents appearing oily; D. Slender hyphae with minute roughening; note clamp connection at right. Scale bars = 10 µm.

not insititious. Rhizomorphs sporadic, white, ropy (not well-defined), associated with resupinate white pad. Taste and odor negligible.

Habitat & phenology: Four collections known, all fruiting on very slender dead twigs of *Tsuga* in southern Appalachian Mountains (Tennessee, South Carolina); June-July.

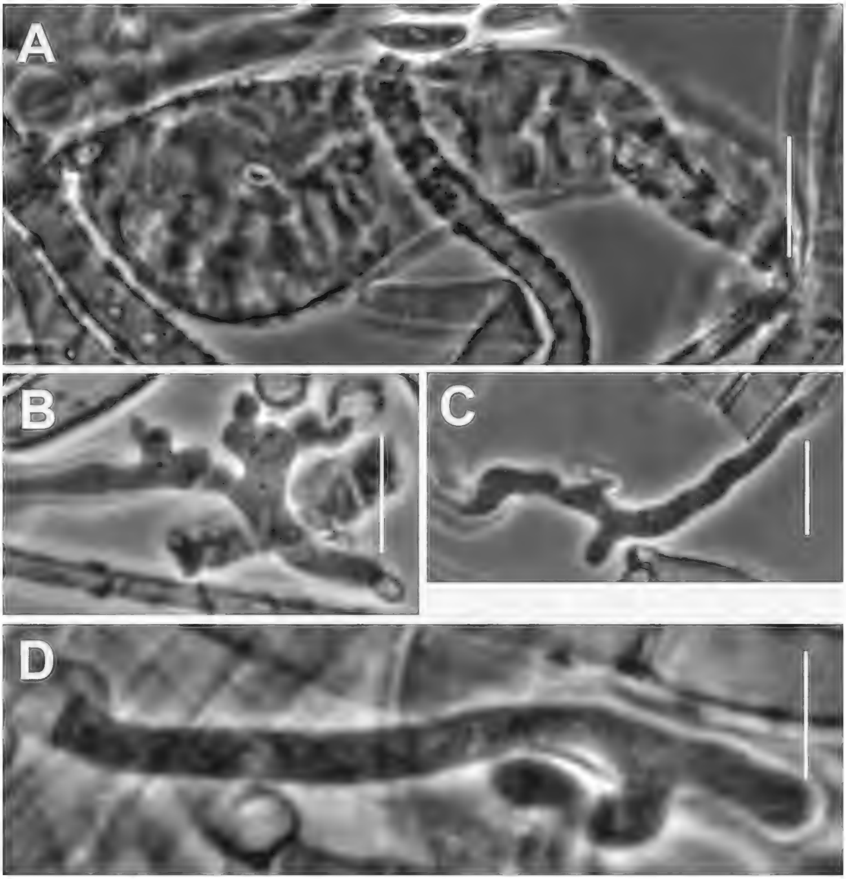


Fig. 44. *Collybiopsis minor*. (TFB 11930; TENN-F-059993). Pileipellis and subpellis hyphae. A. Inflated, ornamented hyphal segment of pileipellis; B-D. Slender, meandering hyphae of subpellis, with occasional lobate side branches. Scale bars = 10 µm.

Pileipellis an interwoven repent layer with no evidence of slime deposition, constructed of the following: 1) repent, unoriented hyphae 3–8.5 µm diam, firm-walled, conspicuously clamped, ranging from smooth (Fig. 43A) to ornamented; ornamentation ranging from a) scattered spiculate "crystals," unoriented; b) annular or striped ornamentation (Fig. 43B) of varying density and width (profile calluses <1 µm thick); contents hyaline, speckled (Fig. 43C) as though oily, to dense and then hypha usually slender (Fig. 43D); 2) inflated hyphal segments (Fig. 44A) <16 µm diam,

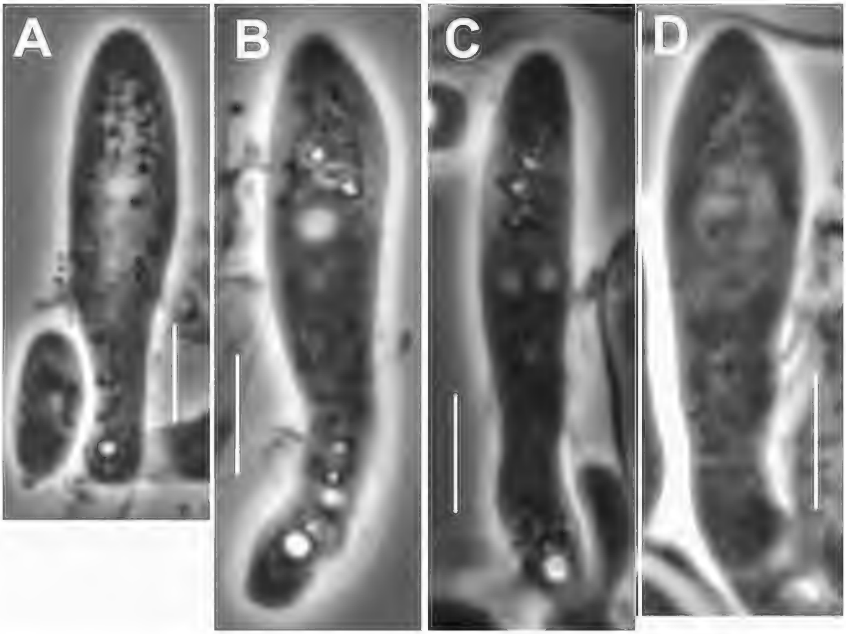


Fig. 45. *Collybiopsis minor*. (TFB 11930; TENN-F-059993). Pleurocystidia (note basidiospore in A). Scale bars = 10 µm.

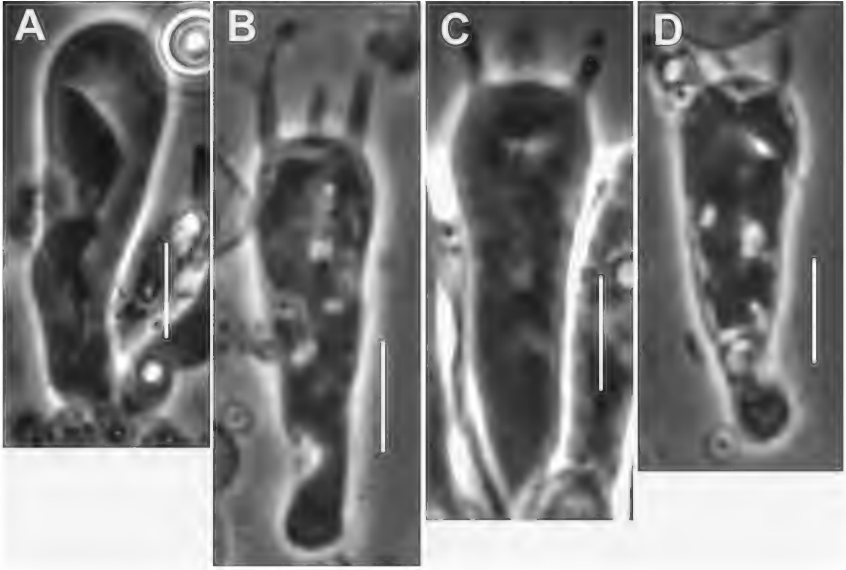


Fig. 46. *Collybiopsis minor*. (TFB 11930; TENN-F-059993). A. Basidiole. B-D. Mature basidia. Note non-refringent, heterogeneous contents. Scale bars = 10 µm.

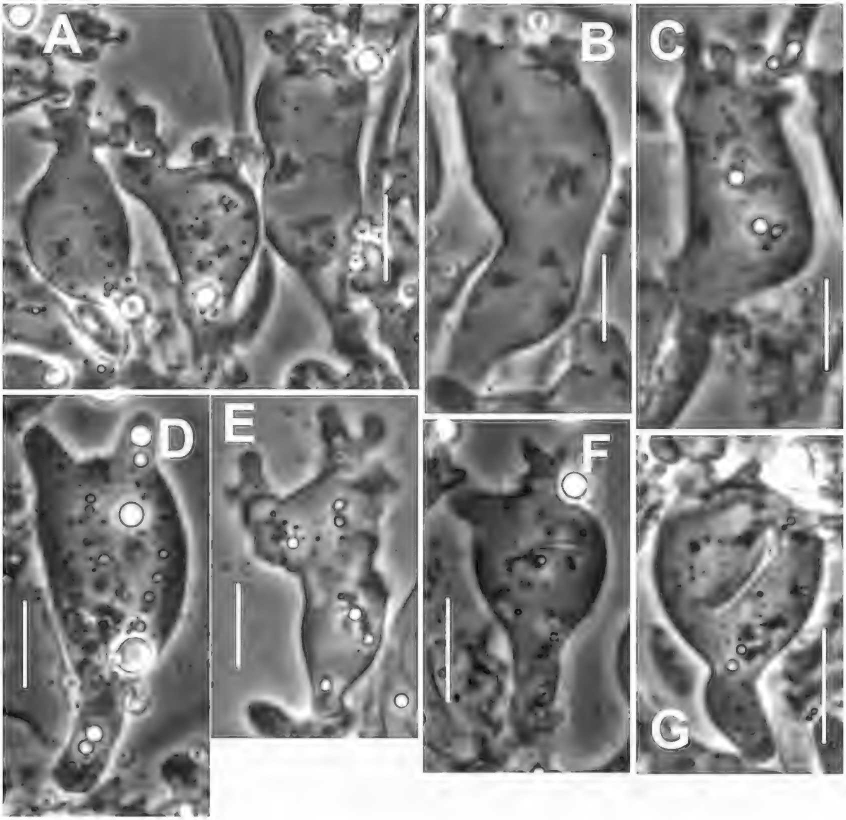


FIG. 47. *Collybiopsis minor*. (TFB 11930; TENN-F-059993). Cheilocystidia. A. Cluster of three cheilocystidia; B, C, E-G. Cheilocystidia with distal prong-like ornamentation; D. Cheilocystidium with two simple sterigmatoid apical lobes. Scale bars = 10 µm.

clavate to keg-shaped, always ornamented with scattered stripes or annular appearance; 3) slender hyphae (FIG. 44B-D), 2.5–4.5 µm diam., firm-walled, often meandering, usually delicately ornamented with spiculate deposits, appearing dense (PhC); and 5) rare cheilocystidium-shaped individuals, 34–46 × 5–7.5 µm, appearing to arise below the subpellis and permeate the pileus surface, clavate, stalked, thick-walled (wall <1.5 µm thick, hyaline) distally pronged to coarsely divided with apical prongs. PLEUROCYSTIDIA (FIG. 45) abundant, 35–45 × 5–8 µm, slender-fusiform to fusiform, hardly discernable from basidioles when immature, conspicuously clamped;

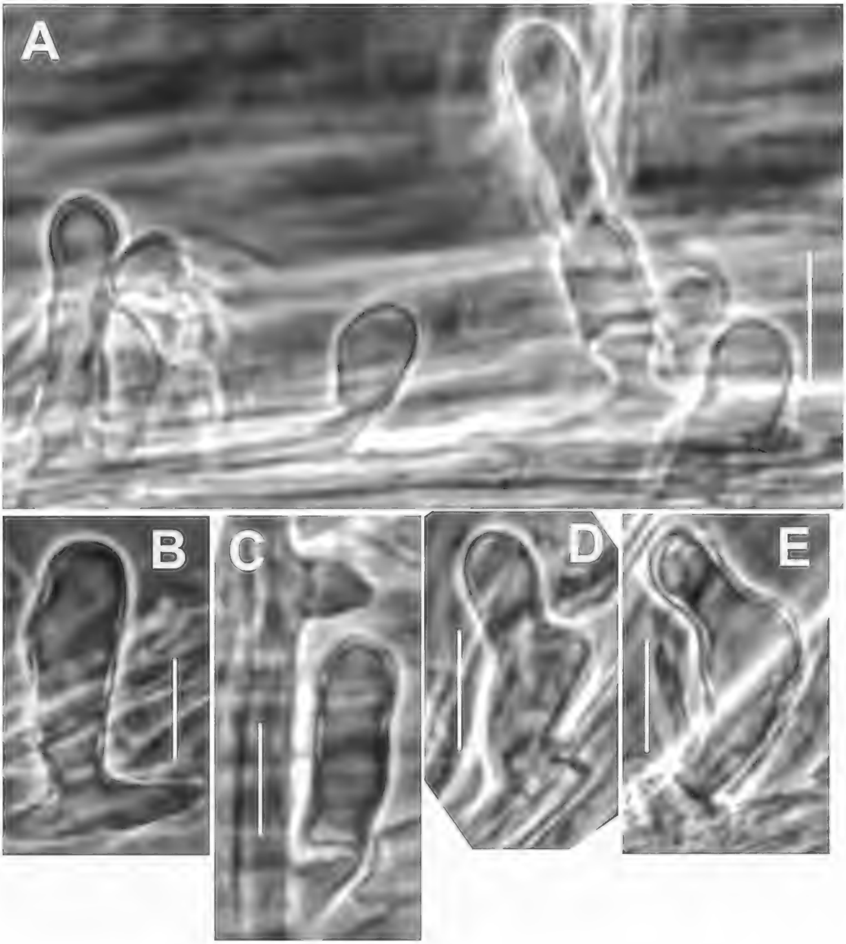


Fig. 48. *Collybiopsis minor*. (TFB 11930; TENN–F-059993). Upper stipe caulocystidia. A. Survey. B-E. Individual caulocystidia. Scale bars = 10 µm.

contents multiguttulate by maturity. Basidioles (Fig. 46A) 30-37 × 7-9 µm (at widest point), clavate, subcapitulate, clamped; contents multiguttulate; basidia (Fig. 46B-D) 30–43 × 7–9 µm, clavate, hardly subcapitulate, 4-sterigmate, clamped; contents mottled, hardly guttulate (not refringent). Basidiospores (Fig. 27) 9–10(–11) × 4–4.5 µm (E = 2.00–2.75; E^m = 2.22; L^m = 9.75 µm), ellipsoid, flattened adaxially, hardly tapered proximally,

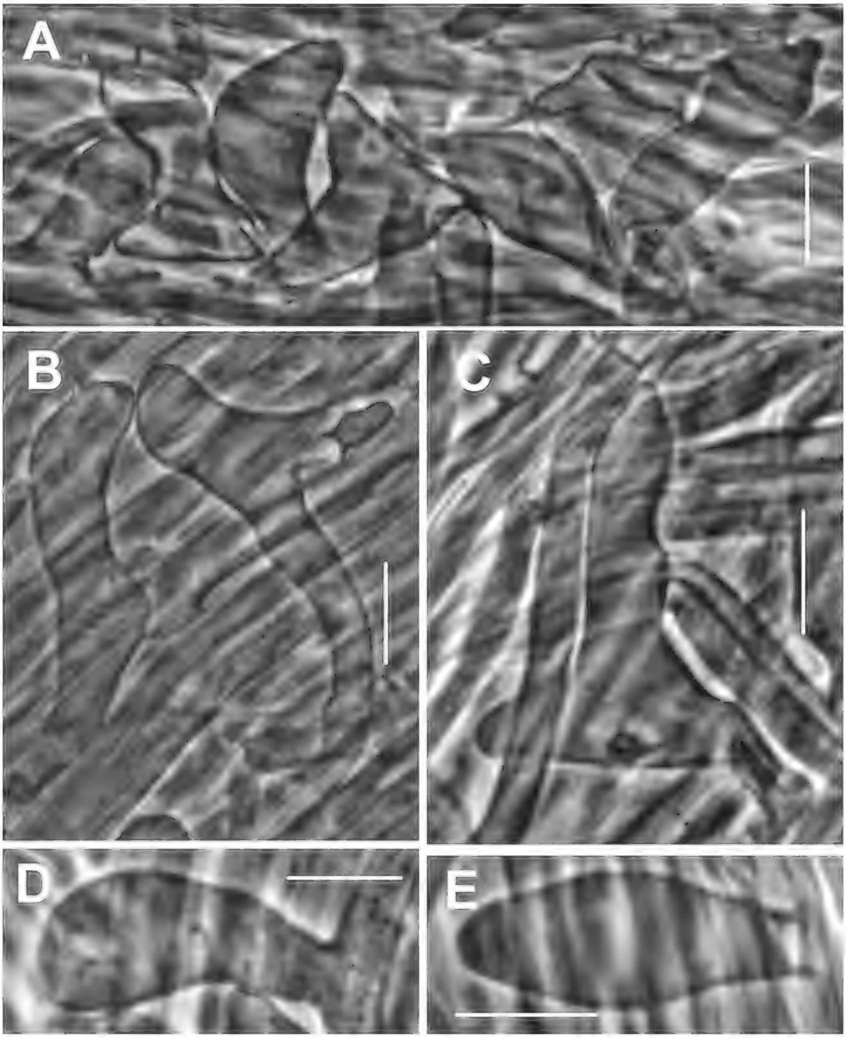


Fig. 49. *Collybiopsis minor*. (TFB 11930; TENN-F-059993). Lower stipe caulocystidia. A. Survey. B-E. Individual caulocystidia. Scale bars = 10 µm.

smooth, thin-walled, inamyloid. Cheilocystidia (Fig. 47) plentiful at lamellar edge, broadly clavate to ventricose-rostrate, firm- to thick-walled (wall <0.5 µm thick, hyaline), 30–55 × 12–20 µm (at widest point); stalk 15–25 × 3.5–5.5 µm, obscurely clamped (easily disarticulated); distal inflated portion subglobose to broadly clavate, ranging from simply lobed (Fig. 47D) to beset with several prong-like protuberances; contents usually multiguttulate (guttules scattered, usually small, refringent PhC). Upper stipe medulla with no evidence of slime or gelatinization; medullary hyphae strictly parallel, of two types: 1) 4–8 µm diam., thick-walled (wall <1.5 µm thick, hyaline), occasionally clamped; 2) 2–3.5 µm diam., thick-walled (wall <0.7 µm thick, hyaline), sometimes meandering, occasionally clamped. Upper stipe cortex similar, weakly pigmented (straw-colored), producing caulocystidia as side branches; caulocystidia (Fig. 48) 5–35 × 4–10 µm (at widest point), papillate, digitate, cylindrical, often swollen at base, not separated from parent hypha by a septum, thick-walled (wall <1.5 µm thick, hyaline). Lower stipe medulla with no evidence of slime or gelatinization; medullary hyphae free (not in slime matrix), strictly parallel, of two types: 1) 3.5–8 µm diam, firm- to thick-walled (wall <0.7 µm thick, hyaline), occasionally clamped; and 2) 2–3.5 µm diam, appearing dense (PhC), frequently clamped, often branched and with "H"-connections. Lower stipe cortex weakly pigmented (straw-colored); cortical cells 3–4.5 µm diam, thick-walled (wall <0.7 µm thick), producing caulocystidia (Fig. 49) as side branches; caulocystidia ranging from broadly fusiform (Fig. 49D, E) to stalked and coarsely lobed (Fig. 49A-C) and inflated <14 µm broad, thick-walled (wall <0.7 µm thick, hyaline), obscurely clamped. Stipe cortex ochraceous-red-brown in IKI + BF.

Commentary: The holotype collection (about 25 basidiomata), originally identified as *Marasmiellus ramealis*, was later revised to *Ma. stenophyllus*. In reality, the pileipellis lacks any *Rameales*-structure, and tramal tissues are devoid of any slime or gelatinous deposition. Similar (but apparently unrelated) are *Marasmiellus synodicus* (Kunze ex Fr.) Singer, a European taxon, and *Marasmius subsynodicus* Murrill, which differs by fruiting on chips and sticks of *Pinus*, distant lamellae, greenish yellow pileus, smaller spores (4–5 × 2 µm, teste Murrill), and more southern distribution. Phylogenetically, *Ma. stenophyllus* appears as sister to a yet-unnamed taxon (MW386874) and more broadly to *Co. quercophila* and *Co. melanopus*.

Additional specimens examined: **USA, North Carolina, Jackson Co.**, vic. Cashiers, trail to Panthertown Valley from Bald Rock, 13.VIII.1993, coll. Nadya Psurtseva & RHP, TFB 10358 (TENN-F-057197). **South Carolina, Oconee Co.**, Walhalla Fish Hatchery, trail to Ellicott Rock, 34°52′58″N 83°20′58″W, 29.VII.1993, coll. RHP, TFB 6284 (TENN-F-052933); Burrell's Ford Campground, 34°52′58″N 83°20′58″W, 12.VIII.2014, coll. HBS class, TFB 14516 (TENN-F-069211).

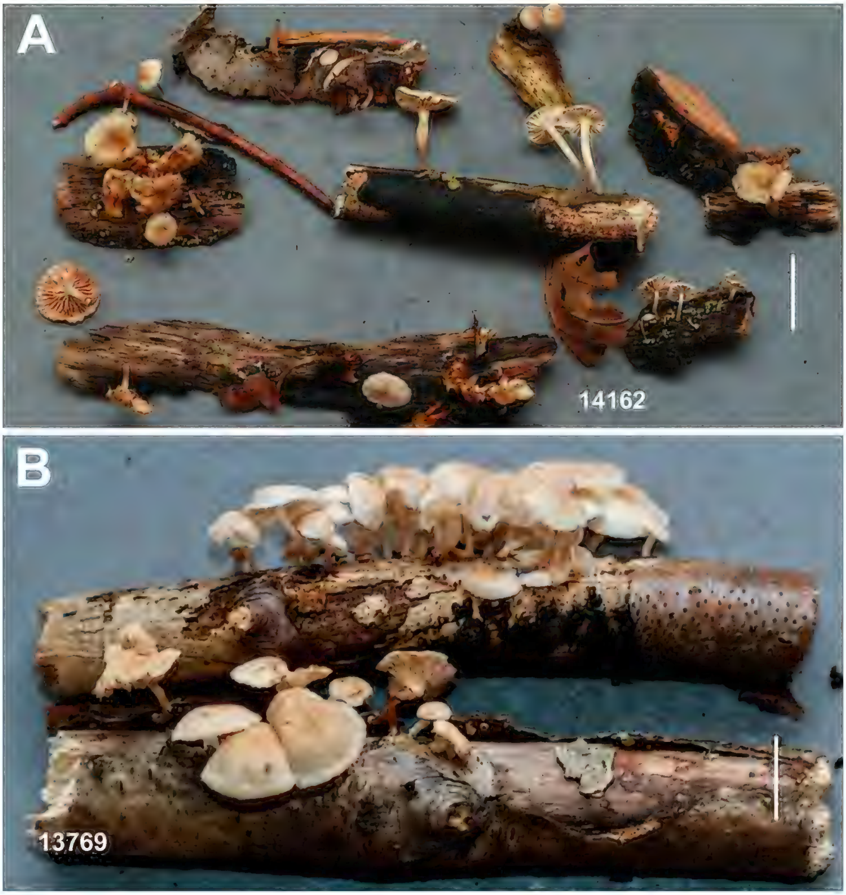


Fig. 50. *Collybiopsis ramealis*. Basidiomata.
A. (TFB 14162; TENN-F-067913). B. (TFB 13769; TENN-F-065145). Scale bars = 10 mm.

Collybiopsis ramealis (Bull.) Millsp.,
West Virginia Geol. Surv. Pt. 1: 127. 1913. Figs 50–60

≡ *Agaricus ramealis* Bull., Herb. France 7: tab no. 336 1788, nom. sanct.

Neotype (designated by Antonín & Noordeloos 1993): France, dept. Pas de Calais, Boulogne sur Mer, 14.X.19873, ME Noordeloos 7310, L.

Epitype (**hic designatus, IF 556205.**): Belgium, Couvin, Damon, Ardennes Mts., River de Rome, 50°01.45′N 4°32.21′W, 8.IX.2010, coll. A Methven, TFB 13769 (TENN-F-065145).

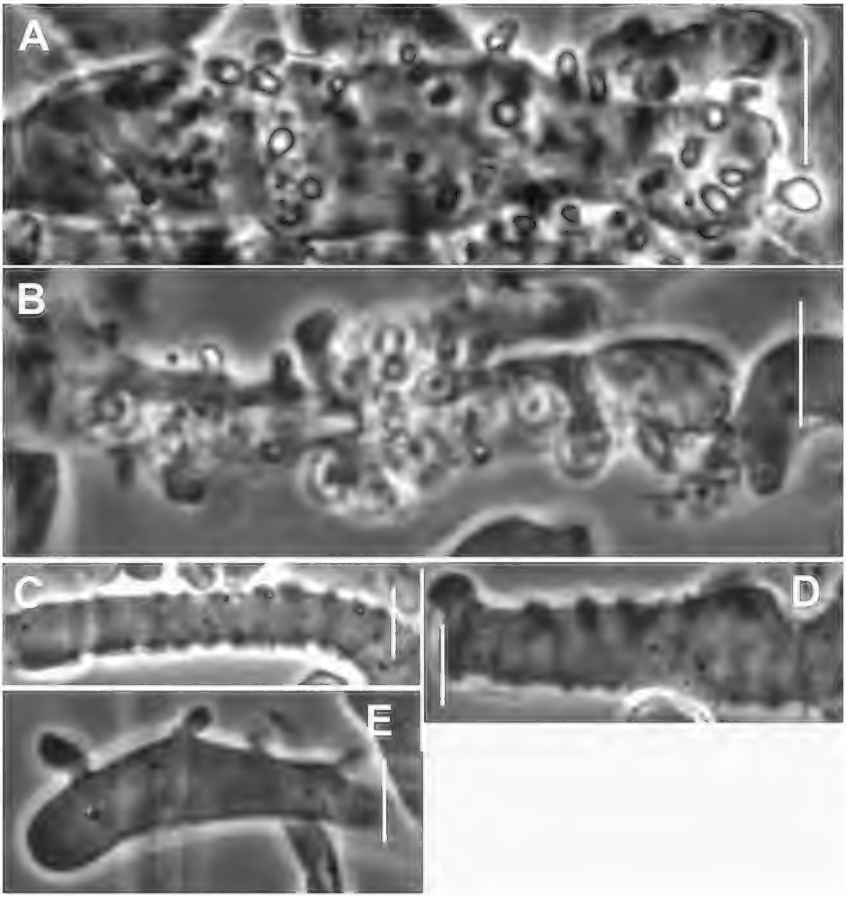


Fig. 51. *Collybiopsis ramealis*. (TFB 14546; TENN-F-069241). Pileipellis elements. A, B, E. Diverticulate hyphae. C, D. Ornamented hyphae. Scale bars = 10 µm.

Basidiomata (Fig. 50) diminutive, gregarious to densely gregarious, occasionally in troops, drying to "ochraceous buff" 5A5 to "wood brown" 7C4. Pileus 3–15 mm broad, matt, shallowly convex to applanate with involute margin, occasionally abruptly umbonate, never umbilicate but irregularly pulvinate, minimally striate at margin, not hygrophanous; disc off-white, "cream buff" 4A4, "light pinkish cinnamon" 7A2, "cinnamon buff" 6B4 to "sayal brown" 6C5, light brown 6D5-6, or paler when young 6D4,"vinaceous buff" 9B2, outward "pinkish buff" 6A3, "pale pinkish cinnamon" 6A2,

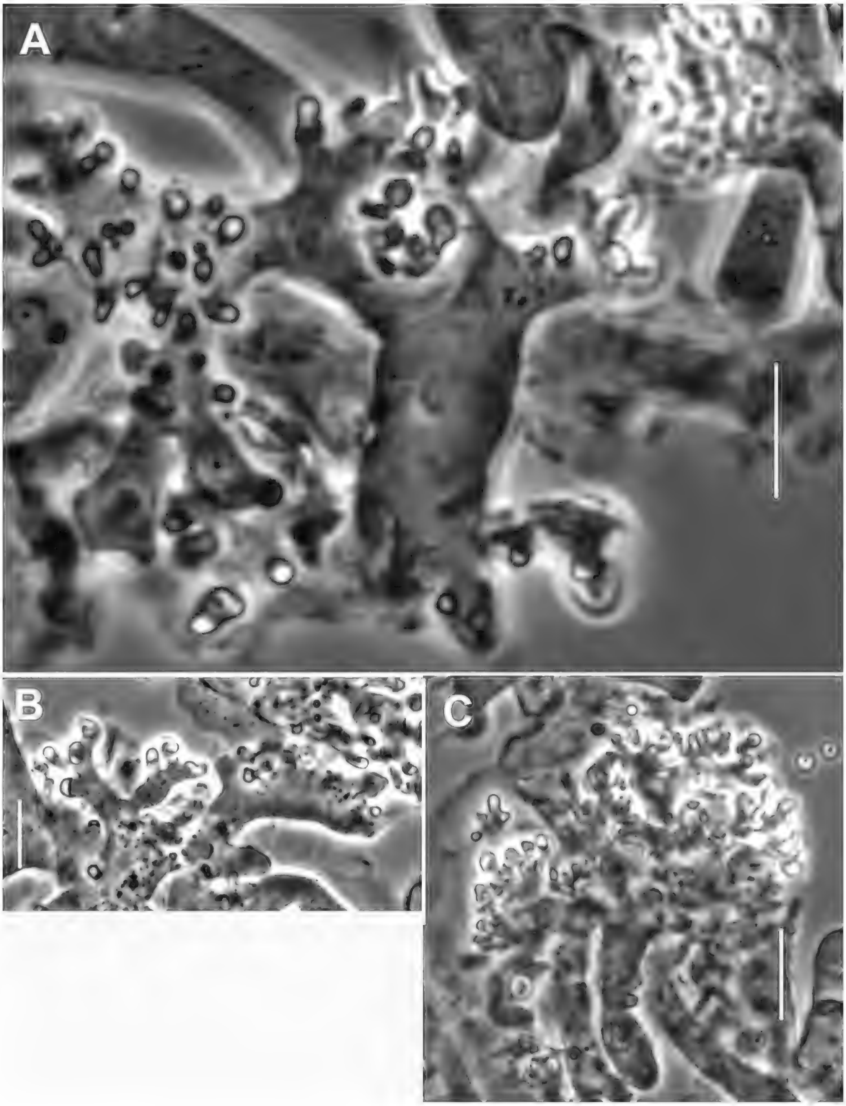


Fig. 52. *Collybiopsis ramealis*. (TFB 14546; TENN-F-069241).
Pileipellis elements; diverticulate hyphal termini. Scale bars = 10 µm.

"pale pinkish buff" 6A2 to "tilleul buff" 7B2, sometimes yellowing in age (orange white 5A2 disc, margin 4A2). Lamellae subdecurrent (and then ending abruptly on stipe), adnexed to adnate to appearing free, more or

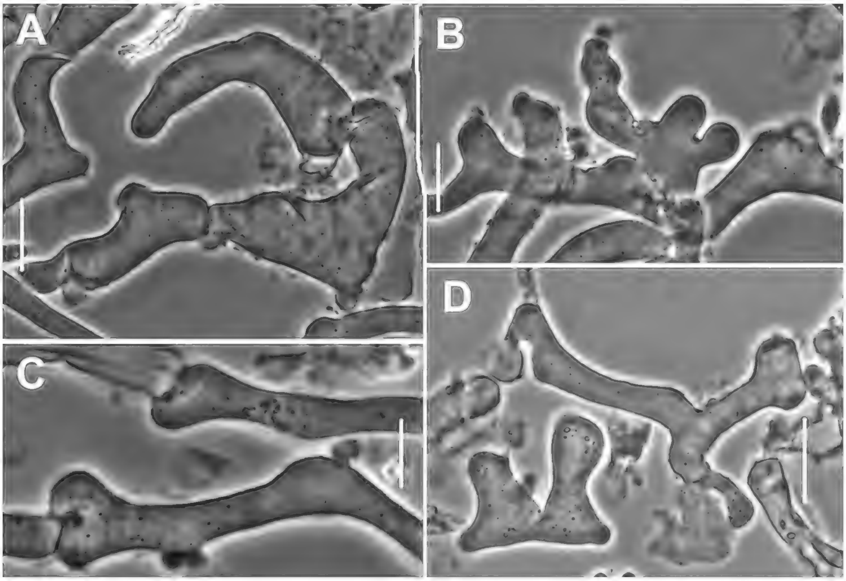


Fig. 53. *Collybiopsis ramealis*. (TFB 14546; TENN-F-069241). Inflated subpellis hyphae. Note prominent clamp connections. Scale bars = 10 µm.

less arcuate, not ventricose, seceding slightly when dried to appear free or pseudocollariate, 0.7-1 mm broad, distant, subdistant to close, (L + ll = 40–43, L = 11–14), thickish, usually concolorous with pileus surface, off-white to "pale pinkish buff" 6A2, "warm buff" 5A4, "pale pinkish cinnamon" 6A2, "pinkish buff" 6A2 with white edge, occasionally suffusing to "light pinkish cinnamon" 7A2 sometimes yellowing in age to "cartridge buff" 30A2 and tending toward crisping in older basidiomata; buttressing rare; anastomosis absent. In normal pilei, hymenophore taking on a fleshy necropigment upon drying. Stipe 6–20 × 1–2 mm broad at apex, equal and remaining so or tapering downward to 0.5-0.8 mm broad at base, inflated apically, there "pale pinkish cinnamon" 6A2, to concolorous with lamellae and minutely flocculose, downward "cream buff" 4A4, "sayal brown" 6C5, "cinnamon buff" 6D4, "vinaceous buff" 9B2, "pinkish cinnamon" 7B5, to "clay color" 5C6, at base "cinnamon buff" 6D4 or "wood brown" 7C4, sometimes yellowing 4A2, "yellow ocher" (orange-white 5A2) and then suffusing light brown 6D4 to brownish orange 6C7, in age occasionally suffusing fleshy cream to "Pompeian red" 10C6 toward base, smooth, without basal pad.

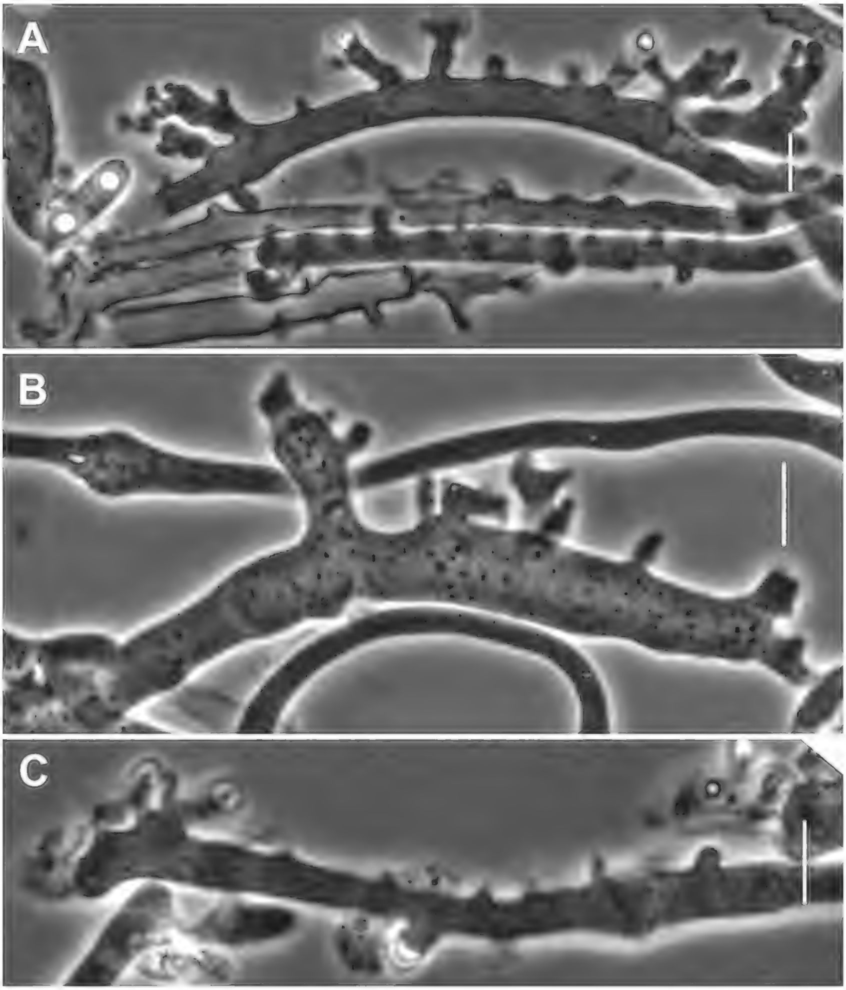


Fig. 54. *Collybiopsis ramealis*. (TFB 14163; TENN-F-067913). Lamellar trama; diverticulate hyphae. Scale bars = 10 µm.

Odor sometimes weakly of garlic or fresh but otherwise negligible; taste not distinctive.

Habitat & phenology: Hardwood (at least *Fagus* or *Quercus*), occasionally on *Rubus* canes, *Crataegus* or other woody substrates, rotting wood, branches, twigs and bark; Europe including Scandinavia and Caucasus; late Summer, early Autumn.

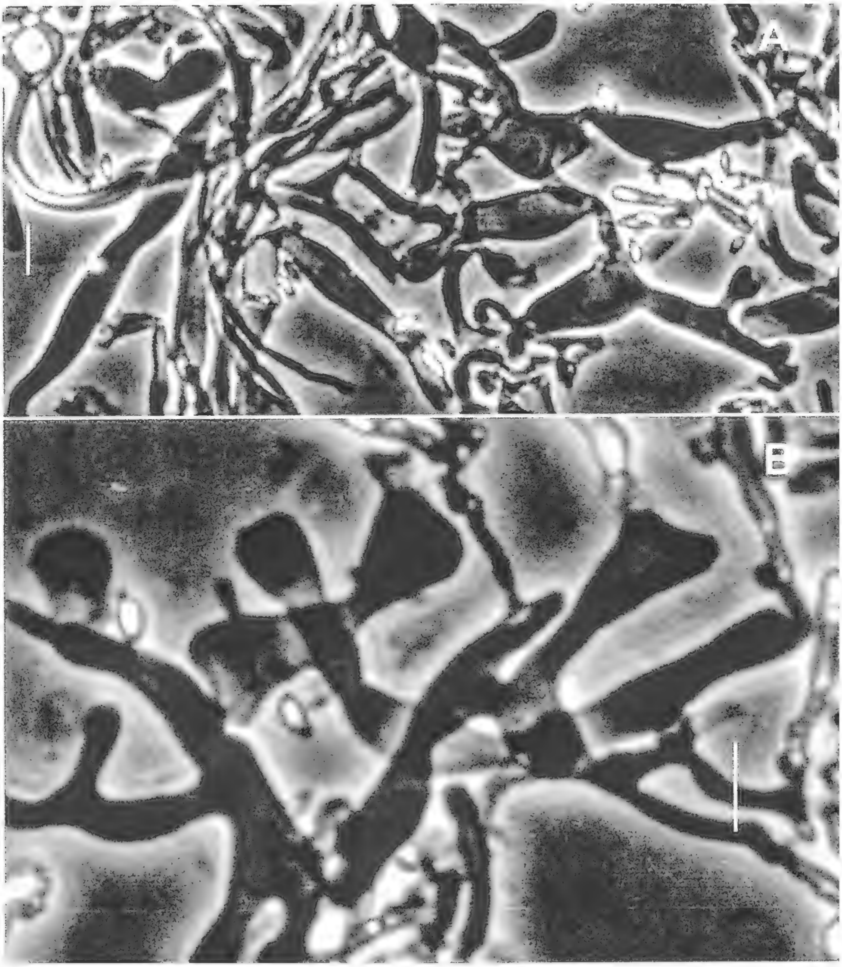


Fig. 55. *Collybiopsis ramealis*. (TFB 14573; TENN-F-069270). Lamellar trama; inflated hyphal segments and termini. Scale bars = 10 µm.

Pileipellis constructed of the following elements: 1) erect filamentous hyphae emerging from subpellis, 25–50 × 4–5 µm, equal to subtly subcapitulate, hyaline, firm-walled, arising as side branches from repent hyphae; 2) antler-shaped hyphae 3–7(–10) µm diam, branched more or less at right angles, often ending in short, blunt, divaricate spurs (tibiiform; *Rameales*-structure; Fig. 51A, B); 3) as above but distinctly ornamented in

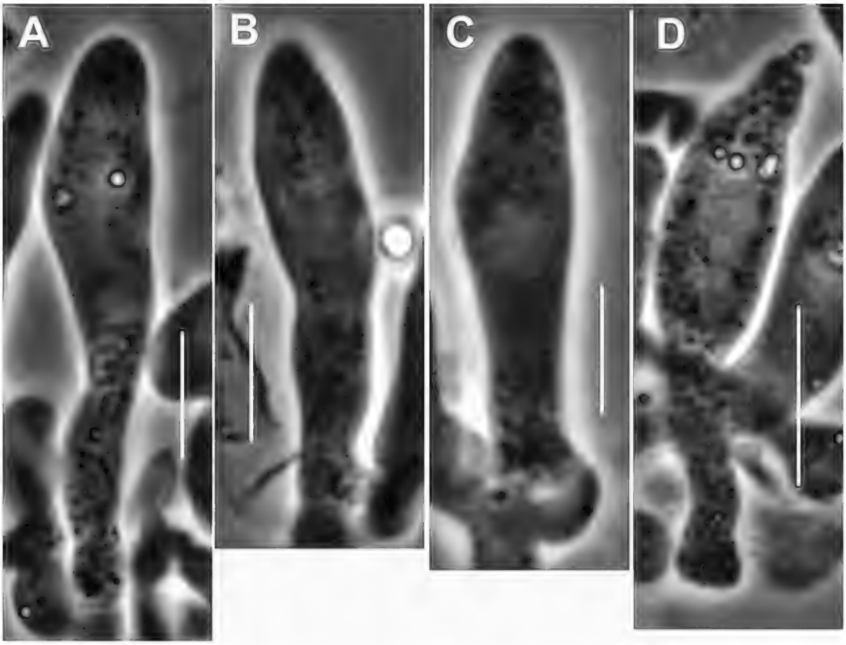


Fig. 56. *Collybiopsis ramealis.* (TFB 14546; TENN-F-069241). Pleurocystidia. Note prominent clamp connection in C. Scale bars = 10 µm.

annular or striped configuration (Fig. 51C, D), always in short lengths; 4) repent hyphae 4–8 µm diam, beset with closely scattered thumb shaped to digitate setulae 1–4 × 0.7–1.0 µm, (Fig. 52B, E) apparently as interseptal hyphal lengths and also as hyphal termini, and then more or less broom cell-like shapes (Fig. 52); setulae as above, often with refringent tips (PhC). Subpellis hyphae loosely interwoven without evidence of slime matrix or sheath, 3.5–15 µm diam (Fig. 53), thin- to firm-walled, conspicuously clamped. Pileipellis near pileus margin a coarse *Rameales*-structure, setulae coarser, knobby, not papillate, closely scattered. Lamellar trama loosely interwoven; hyphae include scattered diverticulate (Fig. 54) and antler-shaped divaricate elements (Fig. 55). Pleurocystidia (Fig. 56) 24–33 × 6–7.5 µm, common to scattered but not normally abundant, digitate (and then difficult to distinguish from basidioles) to narrowly fusiform, conspicuously clamped; contents heterogeneous with scattered granules and often 1–2 refringent inclusions (PhC). Basidioles (Fig. 57A)

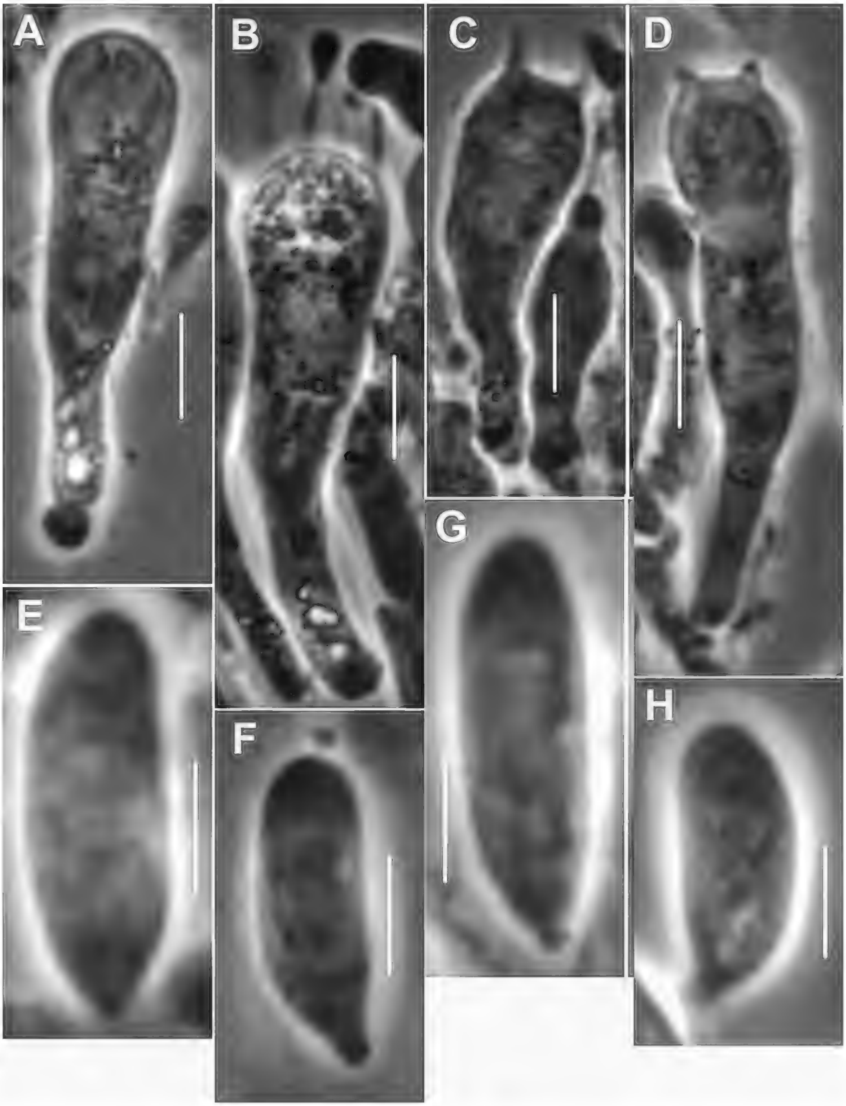


Fig. 57. *Collybiopsis ramealis*. (TFB 13755; TENN-F-065145).
A. Basidiole. B-D. Basidia. E-H. Basidiospores. Scale bars: A–D = 10 µm, E-H = 5 µm.

clavate to subcapitulate. Basidia (Fig. 57B-D) 26–32 × 7–8.5 µm, clavate to subtly subcapitulate, 4-sterigmate (sterigmata very slender, easily collapsed), conspicuously clamped; contents heterogeneous with scattered

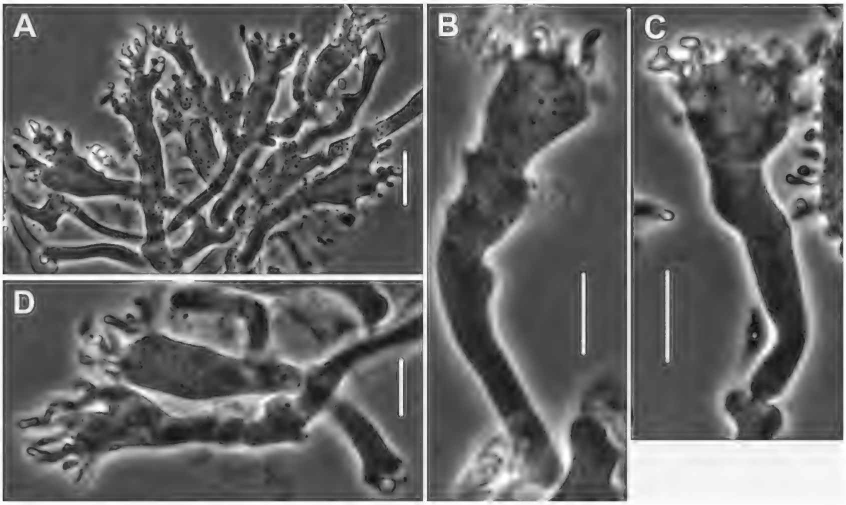


Fig. 58. *Collybiopsis ramealis.* (TFB 14573; TENN-F-069270). Clavate cheilocystidia. Scale bars = 10 µm.

granules. Basidiospores (Fig. 57E-H) (6–)7–10(–11.5) × 2.5–4(–4.5) µm (E= 1.76–3.20; E^m = 2.39; L^m = 8.61 µm), slender ellipsoid, marasmioid (tapered proximally), thin-walled, inamyloid; contents 2–3-guttulate to minutely heterogeneous, appearing foamy. Cheilocystidia (Figs. 58–60) (27–)50–84 × 12–22 µm (at widest point), thickly scattered, often appearing as pseudocystidia (i.e. arising in subhymenium, not in hymenium), ranging from clavate (Fig. 58) to typically long ventricose-rostrate to spheropedunculate with apical setulae (Fig. 59, 60), but occasionally misshapen (Fig. 60), thin- to firm-walled; inflated distal portion pigmented (dark ochraceous, PhC); apical outgrowths ranging from papillate to tentacular/coralloid, apparently flexuous (diverticula, not setulae); stalk slender (1.5–2.5 µm diam), clamped; contents heterogeneous with scattered minute granular aspect. Occasional cheilocystidia clavate (12–15 µm broad, not ventricose-rostrate), beset with scattered papillate setulae. Stipe medullary hyphae strictly parallel, easily extruded in squash mounts, of two types: 1) 4–9 µm diam, thick-walled (wall <1 µm thick, hyaline), conspicuously clamped; and 2) 1–2.5 µm diam, thin- to firm-walled, widely clamped. Stipe cortical hyphae 3–6 µm diam, thick-walled, weakly pigmented (straw-colored PhC), often papillate on outside wall; papillae 0.5–2 × 1 µm, hyaline, thick-walled. Stipe surface

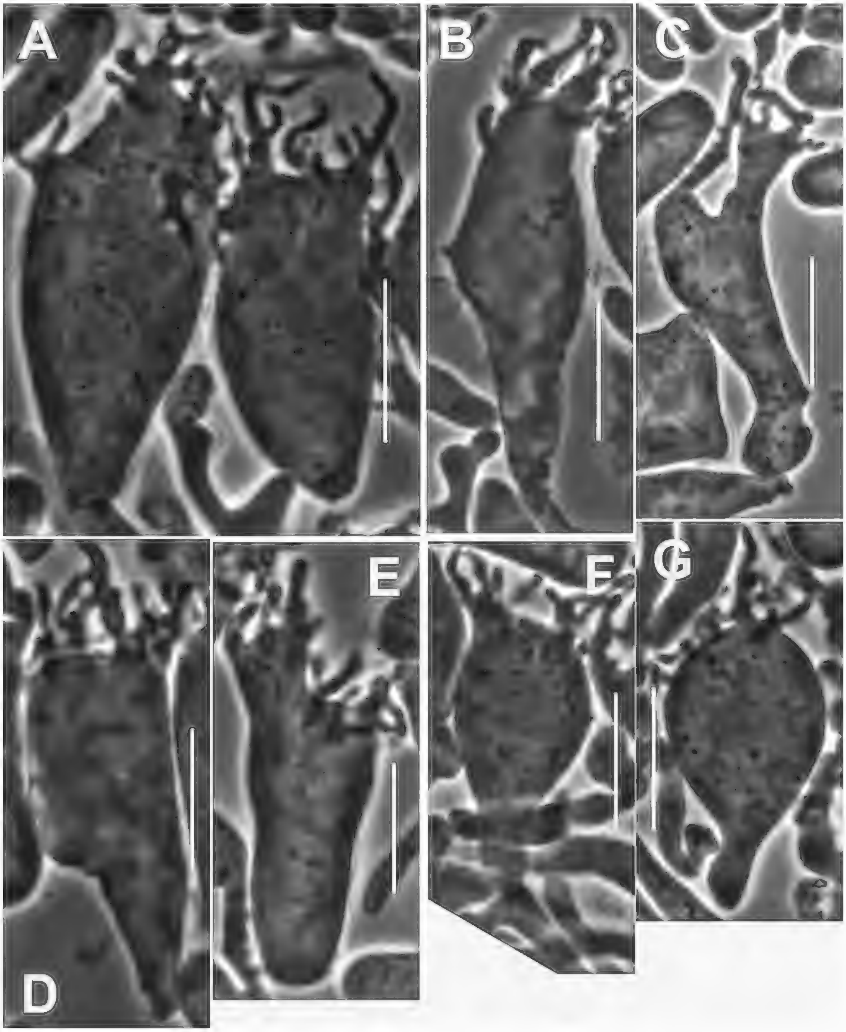


Fig. 59. *Collybiopsis ramealis*. (TFB 14573; TENN-F-069270). Ventricose-rostrate cheilocystidia. Scale bars = 10 µm.

ornamented with utriform to lobate cells arising as thin-walled termini of surface cortical hyphae, 5–10 µm diam. Upper stipe clothed in the following: 1) typical hymenium of basidia, basidioles and occasional pleurocystidia; 2) relatively normal cheilocystidia, but often distorted into odd shapes; and 3) modified cheilocystidia (distinguished by heterogeneous contents and

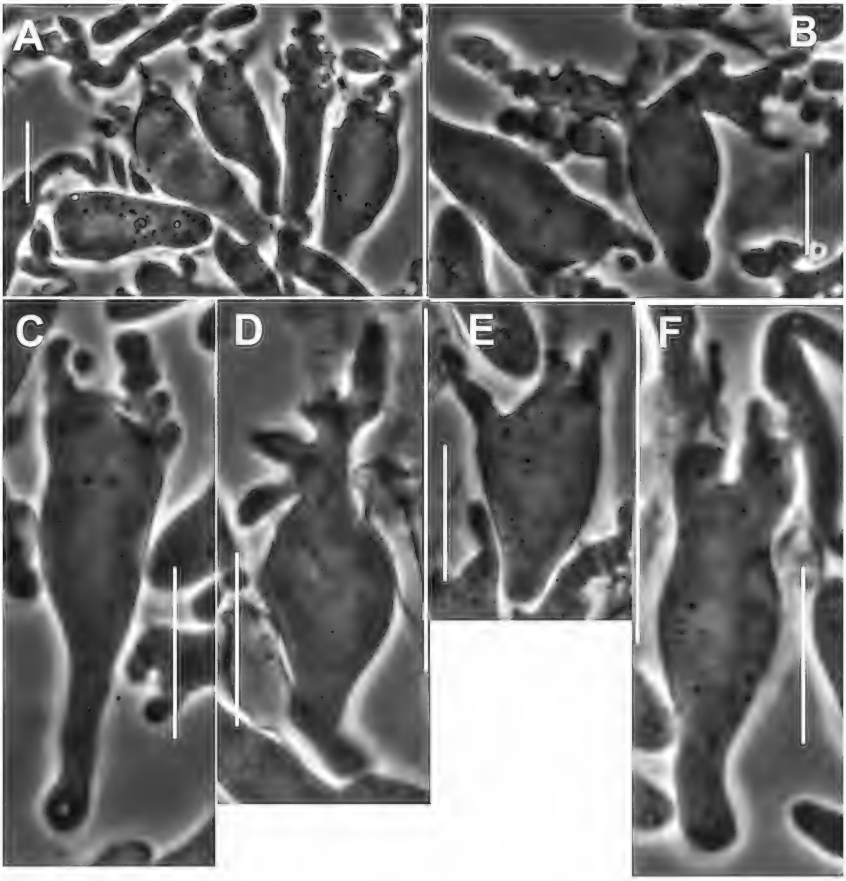


Fig. 60. *Collybiopsis ramealis*. (TFB 14546; TENN-F-069241).
Aberrant clavate cheilocystidia. Scale bars = 10 µm.

very slight pigmentation) into elongate clavate structures 9–13(–19) µm diam (at widest point), appearing as pseudocystidia, smooth to (rarely) beset with apical knobby to coralloid diverticula, firm- to thick-walled (wall <1.0 µm thick, hyaline), with basal clamp connection.

Commentary: Bulliard's illustration clearly shows decurrent, arcuate lamellae (his fig. A) perhaps seceding (his fig. B).

Cheilocystidia of all examined European specimens were pigmented. The pigment is cytoplasmic; the wall is hyaline. Contents are heterogeneous, appearing oily with inclusions (PhC). Contents of basidioles and pleurocystidia are homogeneous but contents of mature basidia are heterogeneous, multigranular with a few small refringent guttules. Based on long pedicel stalks, cheilocystidia seem to arise deep in lamellar trama and project through the lamellar edge. This morphology has been termed "pseudocheilocystidia" (Singer 1968).

Copious spores seem to lodge on lamellar surfaces, especially at the lamellar edge. Other than the projections from cheilocystidial apices, there seems not to be a physical attraction. Spores are usually 2-guttulate; guttules polar (at proximal and distal ends of the spore), and refringent.

While the lamellar edge appears smooth at low magnification, it is delicately serrulate at 250×, with pigmented cheilocystidia appearing dark near or at the lamellar edge.

Stipes vary from terete and equal to compressed and tapering downward to a fine insertion reminiscent of that of *Marasmiellus praeacutus* (see Halling 1987).

Self-crosses were performed on collections TENN-F-052628 (Sweden), TENN-F-065120 (Belgium), TENN-F-065122 (Belgium), TENN-F-065132 (Belgium), and TENN-F-065165 (Belgium). All self-crosses showed tetrapolar mating systems. An intercollection pairing grid developed from single-basidiospore isolates from the Belgian collections showed all collections to be intercompatible, indicating that all belonged to a single mating group.

Earle's explicit assignment of *Marasmius ramealis* as type of his genus *Collybiopsis* did not constitute valid publication of the nomenclatural combination *Collybiopsis ramealis* (ICN Shenzhen Art, 36:2, see also Antonin & Noordeloos 2010: 316), although his intent was indisputable. Millspaugh (1913) made the earliest valid publication of *Collybiopsis ramealis.*

There remains a question about Earle's (1909) use of the AMERICAN CODE OF BOTANICAL NOMENCLATURE (1904, 1907), of which he was a signee, especially Canon 15, embodying the "first species rule." Earle's 1909 effort was intended to be explicitly and exclusively taxonomic, not nomenclatural. In his prose summary he does not mention typification or his method of arriving at the type species of the genera in his generic summary. A search of "Tribe I. Agaricaceae §1. Gymnophylli" (Earle, pp 411-433) covering 73 genera reveals that the preponderance of genera were typified by the first (often the only) species listed in the generic protologue. But in the following, a non-first species was chosen: *Anthracophyllum*, *Leptomyces*, *Prunulus*, *Omphalina*, *Pilacre*, *Lepista*, *Phylloporus*, and *Melanoleuca*. Earle's mechanical use of "The first species rule" (explicit or implicit) cannot be upheld.

But although Earle was not slavish to "the first-species rule" regarding the protologue of the various genera, he was, indeed, slavish in citing Saccardo's Sylloge Fungorum (Vol. 5, covering the agarics). In the various assemblages that Earle recognized as represented in Sylloge, Saccardo's first species do not appear to have been selected as generic types for Earle's genera.

SPECIMENS EXAMINED: **BELGIUM**, Dimonte, vic. Hever, Jemain, Massembre, 50°09′37″N 4°51′29″E, 7.IX.2010, coll. AS Methven, TFB 13755 (TENN-F-065120); coll. S Adamčík, TFB 13745 (TENN-F-065122); vic. Heer, Bois de Baroville, vic. Beauraina, 9.IX.2010, coll. RHP, TFB 13775 (TENN-F-065151); coll. RHP, TFB 13590 (TENN-F-065165); Couvin, Damon, Ardennes Mts., River de Rome, 50°01.45′N 4°32.21′E, 8.IX.2010, coll. A Methven, TFB 13770 (TENN-F-065146). **GERMANY**, **THURINGIA**, vic. Obergebra, off Rte 1016, 51°24.13′N 10°36.05′E, 30.VIII.2012, coll. RHP, TFB 14162 (TENN-F-067912); TFB 14163 (TENN-F-067913); vic. Menteroda, 51°18.18′N 10°33.52′E, 28.VIII.2012, coll. AS Methven, TFB 14140 (TENN-F-067890); Grosslohram vic Nohra, 51°24.40′N 10°36.88′E, 29.VIII.2012, coll. KWH, TFB 14150 (TENN-F-067900). **SLOVAKIA, NITRA**, Prostredny Vrich, Lovce, 48°27′04″N 18°20′49″E, 12.IX.2014, coll. RHP TFB 14573 (TENN-F-069270); Zlate Maravce Dist., vic. Hostie, 48°27′59″N 18°27′35″E, 10.IX.2014, coll A.S. Methven, TFB 14555 (TENN-F-069255); coll A.S. Methven, TFB 14546 (TENN-F-069241). **SWEDEN**, **NÄRKE**, Hjälmarsbaden, Östra Hagen, 59°16.07′N 15°19.07′E, 10.IX.2008, coll. RHP, TFB 13520 (TENN-F-062867); **HALLAND**, Töto Parish, 56°54′19″N 12°47′23″E, 24.IX.1991, coll. SA Gordon, RHP, Stig Jacobsson, TFB 4727 (TENN-F-050324); **UPPLAND**, vic. Uppsala, Fiby Urskog, 59°52′54″N 17°21′13″E, 8.IX.1994, coll. RHP, TFB 7288 (TENN-F-053525); vic. Uppsala, 3IX.1994, coll. unknown, TFB 7248 (TENN-F-052628). **UNITED KINGDOM**, **PERTHSHIRE**, **Pitlochry**, Beach Walk along River Garry & vicinity, 56°42′16″N 3°43′47″W, 2.IX.1997, coll. RHP, TFB 6989 (TENN-F-055908).

Discussion

In future taxonomic investigations, some taxa heretofore described as *Marasmiellus* will be authoritatively sequenced and as a result, will remain securely within *Collybiopsis*. Other sequenced taxa, however, will not remain in *Collybiopsis*, with destinations (e.g., *Marasmiaceae*, *Physalacriaceae*) unpredictable. For example, taxa within *Marasmiellus* sect. *Candidi*, *Ma.* sect. *Stenophylloides*, and *Ma.* sect. *Nigripedes* (= *Tetrapyrgos*) seem destined for *Marasmiaceae* (not *Omphalotaceae-Collybiopsis*, where *Marasmiellus juniperinus* belongs). If done carefully, this process will be slow and piecemeal, inviting caution in blanket transfers.

Here it might be noted that Pegler & Young (1971) cited a specimen of *Ma. juniperinus* from Jamaica (Jamaica, Blue Mountains, 26.XII.1949, Proctor: K). DNA sequences from this specimen might furnish a more secure (topotype) connection for the type of *Marasmiellus*.

The phylogenetic position of *Marasmiellus juniperinus* is unstable and not well-supported by either Olivera & al. (2019) or our analyses. The Olivera & al. (2019) analysis associated *Ma. juniperinus* with TENN-F-068185 (TFB14334; *Gymnopus* sp. 17) and TENN-F-068085 (TFB14228; *Gymnopus* sp.) but without support. Our current analysis associates *Ma. juniperinus* with *Co. quercophila* and *Co. melanopus*, again without support. The underlying cause is that its ITS sequence diverges from the rest of the sequenced taxa in *Collybiopsis* but does not clearly belong elsewhere based on its DNA sequences.

Despite the literature summary presented above (see Introduction), Singer's (1962) acceptance of *Marasmiellus* over *Collybiopsis* is instructive. For many years during the early 20th century an expanded concept of *Marasmius* was accepted, including numerous taxa whose micromorphology did not fully conform to the present circumscription of the genus. Kühner's (1933, 1936) treatments were especially influential. Both *Marasmiellus* and *Collybiopsis* were overlooked as candidates for atypical "*Marasmius*" taxa. In addition, they were also overlooked by some authors (notably Clements & Shear 1931, 1954) who selected type species for many genera. During these years, Singer (1938) used *Hemimycena* for a group of agarics he considered to be without a previous home. It was only later (Singer 1950) when he realized that *Marasmiellus* Murrill 1915 took priority over *Hemimycena* Singer 1938 that *Marasmiellus* came into Singer's purview. In a nomenclatural study of the genera of *Agaricales*, Donk (1962) summarized the history of *Collybiopsis* to that date. There he named a "selected" type species as *Agaricus calopus*. By 1962, Singer had accepted 59 taxa within *Marasmiellus* and, whether before or after Donk's publication, Singer also listed *Agaricus calopus* as type of *Collybiopsis*. The two authors' choice superseded Earle's explicit citation of the generic type for *Collybiopsis* (also distorting Earle's intent), thus steering *Collybiopsis* away from contention for priority over *Marasmiellus*. Both authors, however, also reported that the taxonomic concept of *A. calopus* itself was anything but secure, concluding that *A. calopus* was a "nomen dubium." Singer went one step further: if *A. calopus* was a "nomen dubium," then *Collybiopsis* was also a "nomen dubium." Singer (1962: 417-418) included *Collybiopsis* under "genera imperfectly known." We contend that *Collybiopsis* is in no way a dubious name, having been explicitly established by Earle (1909).

Acknowledgements

We extend our sincere thanks to three anonymous reviewers whose comments and suggestions made this version of the original manuscript stronger. Dr. Else Vellinga caught some substantive errors. Dr. Jerry Cooper, Landcare Research, New Zealand, provided the Millspaugh paper as well as other valuable suggestions. The Mycotaxon Editors excelled in correcting confusing text and formatting and nomenclatural shortcomings; they are sincerely thanked.

APPENDIX I

Collybiopsis recombinations proposed

The correct name for the large clade considered here is *Collybiopsis*, which includes the type species of *Marasmiellus* (*M. juniperinus*), as well as the type species of *Gymnopus* sect. *Vestipedes* (*G. confluens*). Many epithets of appropriate binomials require transfer to *Collybiopsis*. Oliveira & al. (2019) made numerous transfers to *Marasmiellus* but, while we do not disagree with the taxonomy of these transfers, we argue that they are nomenclaturally incorrectly combined in *Marasmiellus* and not *Collybiopsis*. The list of corrected transfers below includes such species epithets with which we have experience but not those which we contend require additional investigation. Based on FIG. 1 (ITS + LSU-based phylogeny), appropriate epithets include those below, but as accurate phylogenetic placement of *Marasmiellus* and *Gymnopus* taxa (and some *Marasmius*) is determined, additional transfers will be necessary.

Collybiopsis biformis (Peck) R.H. Petersen, **comb. nov.**

IF 556182

BASIONYM: *Marasmius biformis* Peck, Bull. 1904 ["1903"]. N.Y. State Mus. 67: 25.
≡ *Marasmiellus biformis* (Peck) J.S. Oliveira. 2019. Mycol. Prog. 18(4): 734.

Collybiopsis brunneigracilis (Corner) R.H. Petersen, **comb. nov.**

IF 557078

BASIONYM: *Marasmius brunneigracilis* Corner. 1996. Nova Hedwigia, Beih. 111: 39.
≡ *Gymnopus brunneigracilis* (Corner) A.W. Wilson, Desjardin, E. Horak. 2004. Sydowia 56(1): 171.
≡ *Marasmiellus brunneigracilis* (Corner) J.S. Oliveira. 2019. Mycol. Prog. 18(5): 734.

Collybiopsis confluens (Pers.) R.H. Petersen, **comb. nov.**

IF 556183

BASIONYM: *Agaricus confluens* Pers. 1796. Observ. Mycol. 1: 8.
≡ *Marasmiellus confluens* (Pers.) J.S. Oliveira. 2019. Mycol. Prog. 18: 734.

Collybiopsis dichroa (Berk. & M.A. Curtis) R.H. Petersen, **comb. nov.**

IF 556184

BASIONYM: *Marasmius dichrous* Berk. & M.A. Curtis. 1853. Ann. Mag. Nat. Hist. 2 12: 426.
≡ *Marasmiellus dichrous* (Berk. & M.A. Curtis) J.S. Oliveira. 2019. Mycol. Prog. 18: 734.

Collybiopsis diminuta (Berk. & Broome) R.H. Petersen, **comb. nov.**

IF 56185

BASIONYM: *Agaricus diminutus* Berk. & Broome. 1871. J. Linn. Soc., Bot. 11: 251.

Collybiopsis disjuncta (R.H. Petersen & K.W. Hughes) **comb. nov.**

IF 556777

BASIONYM: *Gymnopus disjunctus* R.H. Petersen & K.W. Hughes. 2014. N. Am. Fung. 9: 2.
≡ *Marasmiellus disjunctus* (R.H. Petersen & K.W. Hughes) J.S. Oliveira. 2019. Mycol. Prog. 18: 734.

Collybiopsis eneficola (R.H. Petersen) R.H. Petersen, **comb. nov.**

IF 556186

Basionym: *Gymnopus eneficola* R.H. Petersen. 2014. Omphalina 5(5): 5.

≡ *Marasmiellus eneficola* (R.H. Petersen) J.S. Oliveira. 2019. Mycol. Prog. 18: 734.

Collybiopsis fibrosipes (Berk. & M.A. Curtis) R.H. Petersen, **comb. nov.**

IF 557077

Basionym: *Marasmius fibrosipes* Berk. & M.A. Curtis. 1869. J. Linn. Soc. Bot. 10: 293.

≡ *Collybia fibrosipes* (Berk. & M.W. Curtis) Dennis. 1951. Trans. Brit. Mycol. Soc. 34(4): 448

≡ *Gymnopus fibrosipes* (Berk. & M.A. Curtis) J.L. Mata. 2003 Mycotaxon 86: 315.

Collybiopsis foliiphila (A.K. Dutta, K. Acharya & Antonín) R.H. Petersen, **comb. nov.**

IF 557080

Basionym: *Marasmiellus foliiphilus* A.K. Dutta, K. Acharya & Antonín. 2015. Mycol. Prog. 14: 5.

Collybiopsis gibbosa (Corner) R.H. Petersen, **comb. nov**.

IF 556187

Basionym: *Marasmius gibbosus* Corner. 1996. Nova Hedwigia, Beih. 111: 53.

≡ *Marasmiellus gibbosus* (Corner) J.S. Oliveira. 2019. Mycol. Prog. 18: 734.

Collybiopsis indocta (Corner) R.H. Petersen, **comb. nov.**

IF 556188

Basionym: *Marasmius indoctus* Corner. 1996. Nova Hedwigia, Beih. 111: 60.

≡ *Marasmiellus indoctus* (Corner) J.S. Oliveira. 2019. Mycol. Prog. 18: 735.

Collybiopsis juniperina (Murrill) R.H. Petersen, **comb. nov.**

IF 556189

Basionym: *Marasmiellus juniperinus* Murrill. 1915 N. Am. Fl. 9(4): 243.

Collybiopsis luxurians (Peck) R.H. Petersen, **comb. nov**.

IF 556190

Basionym: *Collybia luxurians* Peck. 1897. Bull. Torrey Bot. Club 24: 141.

≡ *Marasmiellus luxurians* (Peck) J.S. Oliveira. 2019. Mycol. Prog. 18: 735.

Collybiopsis melanopus (A.W. Wilson, Desjardin & E. Horak) R.H. Petersen, **comb. nov**.

IF 556191

Basionym: *Gymnopus melanopus* A.W. Wilson, Desjardin & E. Horak. 2004. Sydowia 56: 181

≡ *Marasmiellus melanopus* (A.W. Wilson, Desjardin & E. Horak) J.S. Oliveira. 2019. Mycol. Prog. 18: 735

Collybiopsis menehune (Desjardin, Halling & Hemmes) R.H. Petersen, **comb. nov.**

IF 556192

Basionym: *Gymnopus menehune* Desjardin, Halling & Hemmes. 1999. Mycologia 91(1): 173.

≡ *Marasmiellus menehune* (Desjardin, Halling & Hemmes) J.S. Oliveira. 2019. Mycol. Prog. 18: 375.

Collybiopsis mesoamericana (J.L. Mata) R.H. Petersen, **comb. nov.**

IF 556193

Basionym: *Gymnopus mesoamericanus* J.L. Mata. 2006. Sydowia 58(2): 283.

≡ *Marasmiellus mesoamericanus* (J.L. Mata) J.S. Oliveira. 2019. Mycol. Prog. 19: 735.

Collybiopsis micromphaloides (R.H. Petersen & K.W. Hughes) R.H. Petersen, **comb. nov.**

IF 556778

Basionym: R.H. Petersen & K.W. Hughes. 2014. N. Am. Fungi 9: 6.

≡ *Marasmiellus micromphalioides* (R.H. Petersen & K.W.Hughes) J.S. Oliveira. 2019. Mycol. Prog. 18: 735.

Collybiopsis neotropica (Singer) R.H. Petersen, **comb. nov.**

IF 556942

Basionym: *Collybia neotropica* Singer. 1962 [“1961”]. Sydowia 15: 54.

≡ *Gymnopus neotropicus* (Singer) J.L. Mata. 2003. Mycotaxon 86:313.

≡ *Marasmiellus neotropicus* (Singer) J.S. Oliveira. 2019. Mycol. Prog. 18: 735.

Collybiopsis nonnulla (Corner) R.H. Petersen, **comb. nov.**

IF 556194

Basionym: *Marasmius nonnullus* Corner. 1996, Nova Hedwigia, Beih. 111: 76.

≡ *Marasmiellus nonnullus* (Corner) J.S. Oliveira 2019, Mycol. Prog. 18: 735.

Collybiopsis obscuroides (Antonín & Legon) R.H. Petersen, **comb. nov.**

IF 556943

Basionym: *Gymnopus obscuroides* Antonín & Legon. 2008. Czech Mycol. 60: 14.

Collybiopsis parvula (J.L. Mata, R.H. Petersen & K.W. Hughes) R.H. Petersen, **comb. nov.**

IF 556779

Basionym: *Gymnopus parvulus* J.L. Mata, R.H. Petersen & K.W. Hughes. 2007. Sydowia 58(2): 285.

≡ *Marasmiellus parvulus* (J.L. Mata, R.H. Petersen & K.W. Hughes) J.S. Oliveira. 2019. Mycol. Prog. 18: 735.

Collybiopsis peronata (Bolton) R.H. Petersen, **comb. nov.**

IF 556195

Basionym: *Agaricus peronatus* Bolton. 1788. Hist. Fung. Halifax 2: 58.

≡ *Marasmiellus peronatus* (Bolton) J.S. Oliveira. 2019. Mycol. Prog. 18: 735.

Collybiopsis polygramma (Mont.) R.H. Petersen, **comb. nov.**

IF 556944

Basionym: *Marasmius polygrammus* Montagne. 1854. Ann. Sci. Nat, Bot. ser. 4 1: 118.

≡ *Gymnopus polygrammus* (Mont.) J.L. Mata. 2003. Mycotaxon 86: 313.

≡ *Marasmiellus polygrammus* (Mont.) J.S. Oliveira. 2019. Mycol. Prog. 18: 735.

Collybiopsis pseudoluxurians (R.H. Petersen & K.W. Hughes) R.H. Petersen, **comb. nov.**

IF 556196

Basionym: *Gymnopus pseudoluxurians* R.H. Petersen & K.W. Hughes. 2014, N. Am. Fung. 9(3): 7.

≡ *Marasmiellus pseudoluxurians* (R.H. Petersen & K.W. Hughes) J.S. Oliveira. 2019. Mycol. Prog. 19: 736

Collybiopsis quercophila (Pouzar) R.H. Petersen, **comb. nov.**

IF 556197

Basionym: *Marasmius quercophilus* Pouzar. 1982. Česka Mykol. 36(1): 1.

≡ *Marasmiellus quercophilus* (Pouzar) J.S. Oliveira. 2019. Mycol. Prog. 18: 735.

Collybiopsis readiae (G. Stev.) R.H. Petersen, **comb. nov.**

IF 556945

Basionym: *Crinipellis readiae* G. Stev. 1964. Kew Bull. 19(1): 43.

≡ *Gymnopus readiae* (G. Stev.) J.L. Mata. 2007. Sydowia 58: 289.

Collybiopsis stenophylla (Mont.) R.H. Petersen, **comb. nov.**

IF 557079

Basionym: *Marasmius stenophyllus* Mont. 1854. Ann. Sci. Nat., Bot.Ser. 4 1: 116.

≡ *Marasmiellus stenophyllus* (Mont.) Singer. 1962. Sydowia 15: 58.

≡ *Gymnopus stenophyllus* (Mont.) J.L. Mata & R.H. Petersen. 2004. Mycoscience 45(1): 221.

Collybiopsis subcyathiformis (Murrill) R.H. Petersen, **comb. nov.**

IF 556946

Basionym: *Marasmius subcyathiformis* Murrill. 1915. N. Amer. Fl. 9(4): 269.

≡ *Marasmiellus subcyathiformis* (Murrill) J.S. Oliveira. 2019. Mycol. Prog. 18: 735.

≡ *Gymnopus subcyathiformis* (Murrill) Desjardin, Halling & Hemmes. 1999. Mycologia 91: 175.

Collybiopsis subnuda (Ellis ex Peck) R.H. Petersen, **comb. nov.**

IF 556198

Basionym: *Marasmius subnudus* Ellis ex Peck. 1898. Bull. Torrey Bot. Club 25: 287.

≡ *Marasmiellus subnudus* (Ellis ex Peck) J.S. Oliveira. 2019. Mycol. Prog. 18: 735.

Collybiopsis subpruinosa (Murrill) R.H. Petersen, **comb. nov.**

IF 556199

Basionym: *Marasmius subpruinosus* Murrill. 1915. N. Amer. Fl. 9: 266.

≡ *Marasmiellus subpruinosus* (Murrill) J.S. Oliveira. 2019. Mycol. Prog. 18: 735.

Collybiopsis synodica (Kunze ex Fr.) R.H. Petersen, **comb. nov.**

IF 556200

Basionym: *Agaricus synodicus* Kunze ex Fr. 1830. Linnaea 5: 507.

Collybiopsis termiticola (Corner) R.H. Petersen, **comb. nov.**

IF 556201

Basionym: *Marasmius termiticola* Corner. 1996. Nova Hedwigia. Beih. 111: 101.
≡ *Marasmiellus termiticola* (Corner) J.S. Oliveira. 2019. Mycol. Prog. 18: 736.

Collybiopsis vaillantii (Pers.) R.H. Petersen, **comb. nov.**

IF 556202

Basionym: *Agaricus ericetorum* β *vaillantii* Pers. 1801. Syn. Meth. Fung. 2: 472.

Collybiopsis villosipes (Cleland) R.H. Petersen, **comb. nov.**

IF 556203

Basionym: *Marasmius villosipes* Cleland. 1934.
Toadstools Mushrooms S. Austral. 1: 166.
≡ *Marasmiellus villosipes* (Cleland) J.S. Oliveira. 2019. Mycol. Prog. 18: 736.

Literature cited

Aldrovandi MSP, Johnson JE, O'Meara B, Petersen RH, Hughes KW. 2015. *Xeromphalina campanella/kauffmanii* complex: species delineation and biogeographical patterns of speciation. Mycologia 107(6): 1270–1284. https://doi.org/10.3852/15-087

Anonymous. 1904. American Code of Botanical Nomenclature. Bull. Torrey Bot. Club 31: 249–261.

Anonymous. 1907. American Code of Botanical Nomenclature. Bull. Torrey Bot. Club 34: 167–178.

Antonín V, Noordeloos ME. 1993. A monograph of *Marasmius*, *Collybia* and related genera in Europe. Part. I: *Marasmius*, *Setulipes*, and *Marasmiellus*. Libri Botanici 8. IHW-Verlag. 229 p.

Antonín V, Noordeloos ME. 1997. A monograph of *Marasmius*, *Collybia* and related genera in Europe. Part 2: *Collybia*, *Gymnopus*, *Rhodocollybia*, *Crinipellis*, *Chaetocalathus* and additions to *Marasmiellus*. Libri Botanici 17. IHW-Verlag. 256 p.

Antonín V, Noordeloos ME. 2010. A monograph of marasmioid and collybioid fungi found in Europe. HW Verlag. 478 p.

Bergemann SE, Garbelotto M. 2006. High diversity of fungi recovered from the roots of mature tanoak (*Lithocarpus densiflorus*) in northern California. Botany 84(9): 1380–1394. https://doi.org/10.1139/b06-097

Binder M, Hibbett DS. 2002. Higher-level phylogenetic relationships of *Homobasidiomycetes* (mushroom-forming fungi) inferred from four rDNA regions. Mol. Phylog. Evol. 22(1): 76–90. https://doi.org/10.1006/mpev.2001.1043

Clements FE, Shear CL. 1931. The genera of fungi. Noble Offset & Printing, N.Y. Hafner Publ. Co., N.Y.

Clements FE, Shear CL. 1954. The genera of fungi. 2nd printing. Hafner Publ. Co.

Corner EJH. 1996. The agaric genera *Marasmius*, *Chaetocalathus*, *Crinipellis*, *Heimiomyces*, *Resupinatus*, *Xerula* and *Xerulina* in Malasia. Nova Hedwigia, Beih. 111. 175 p.

Dentinger BTM, Gaya E, O'Brien H, Suz LM, Lachlan R, Diaz-Valderrama JR, Koch RA, Aime MC. 2016. Tales from the crypt: genome mining from fungarium specimens improves resolution of the mushroom tree of life. Biol. J. Linn. Soc. 117: 1–22. https://doi.org/10.1111/bij.12553

Desjardin DE. 1987. New and noteworthy marasmioid fungi from California. Mycologia 79(1): 123–134. https://doi.org/10.1080/00275514.1987.12025378

Desjardin DE. 1997. A synopsis of *Marasmiellus* in the southern Appalachian Mountains. Mycotaxon 65: 237–261.

Desjardin DE, Perry BA. 2017. The gymnopoid fungi (*Basidiomycota*, *Agaricales*) from the Republic of São Tomé and Príncipe, West Africa. Mycosphere 8(9): 1317–1391. https://doi.org/10.5943/mycosphere/8/9/5

Desjardin DE, Perry BA, Shay JF, Newman DS, Randrianjohany E. 2017. The type species of *Tetrapyrgos* and *Campanella* (*Basidiomycota*, *Agaricales*) are redescribed and epitypified. Mycosphere 8(8): 977–985. https://doi.org/10.5943/mycosphere/8/8/1

Donk MA. 1962. The generic names proposed for *Agaricaceae*. Nova Hedwigia, Beih. 5. 320 p.

Dutta AK, Wilson AW, Antonín V, Acharya K. 2015. Taxonomic and phylogenetic study of gymnopoid fungi from eastern India. I. Mycol. Prog. 14: 1-18. https://doi.org/10.1007/s11557-015-1094-3

Earle FS. 1909. The genera of the North American gill fungi. Bull. N. Y. Bot. Gard. 5: 373–462.

Geneious. 2017. Geneious version 11.0.3 created by Biomatters. Available from http://www.geneious.com/.

Halling, RE. 1987. Studies on *Marasmiellus* (*Tricholomataceae*) in the United States, I. A new species and a new combination. Syst. Bot. 12(3): 400–405. https://doi.org/10.2307/2419264

Honan A, Desjardin DE, Perry BA, Horak E, Baroni TJ. 2015. Towards a better understanding of *Tetrapyrgos* (*Basidiomycota*, *Agaricales*): new species, type studies, and phylogenetic inferences. Phytotaxa 23(2): 101–132. https://doi.org/10.11646/phytotaxa.231.2.1

Horak E. 1968. Synopsis generum Agaricalium. Beitr. Kryptogam. Schweiz 13. 747 p.

Horak E. 1971. A contribution towards the revision of the *Agaricales* (fungi) from New Zealand. New Zealand J. Bot. 9(3): 463–493. https://doi.org/10.1080/0028825X.1971.10430194

Hughes KW, Petersen RH. 2015. Transatlantic disjunction in fleshy fungi. III. *Gymnopus confluens*. MycoKeys 9: 37–63. https://doi.org/10.3897/mycokeys.9.4700

Hughes KW, Petersen RH, Johnson JE, Moncalvo J-M, Vilgalys R, Redhead SA, Thomas T, McGhee LL. 2001. Infragenic phylogeny *Collybia* s. str. based on sequences of ribosomal ITS and LSU regions. Mycol. Res. 105: 164–172. https://doi.org/10.1017/S0953756200003415

Hughes KW, Petersen RH, Mata JL, Psurtseva NV, Kovalenko AE, Morozova OV & al. 2008 (“2007”) *Megacollybia* (*Agaricales*). Rep. Tottori Mycol. Inst. 45: 1–57.

Hughes KW, Reboredo-Segovia A, Petersen RH. 2014. Transatlantic disjunction in fleshy fungi. I. The *Sparassis crispa* complex. Mycol. Progr. 13: 407–427. https://doi.org/10.1007/s11557-013-0927-1

Hughes KW, Reboredo-Segovia A, Morris SD. 2015. Cloning of ribosomal ITS PCR products creates frequent, non-random chimeric sequences - a test involving a heterozygotes between *Gymnopus dichrous* taxa I and II. MycoKeys 10: 45–56. https://doi.org/10.3897/mycokeys.10.5126

Huelsenbeck J, Ronquist F. 2001. MrBayes: Bayesian Inference of phylogenetic trees. Bioinformatics 17:754–755. https://doi.org/10.1093/bioinformatics/17.8.754

Kerekes J, Desjardin DE. 2009. A monograph of the genera *Crinipellis* and *Moniliophthora* from Southeast Asia including a molecular phylogeny of the nrITS region. Fung. Div. 37: 101–152.

Kim CS, Jo JW, Kwag Y-N, Sung G-H, Lee S-G, Kim S-Y, Shin C-H, Han S-K. 2015. Mushroom flora of Ulleug-gun and a newly recorded *Bovista* species in the Republic of Korea. Microbiology 43(3): 239–259. https://doi.org/10.5941/MYCO.2015.43.3.239

Kluber LA, Smith JE, DD Myroid DD. 2011. Distinctive fungal and bacterial communities are associated with mats formed by ectomycorrhizal fungi. Soil Biol. Biochem. 43(5): 1042–1050. https://doi.org/10.1016/j.soilbio.2011.01.022

Kornerup A, Wanscher JH 1967. Methuen handbook of colour. Methuen & Co., 243 pp + 30 plates.

Kühner R 1933 Étude sur le genre *Marasmius*. Le Botaniste 25: 57–116.

Kühner R 1936. Nouvelles recherches sur le genre *Marasmius*. Ann. Soc. Linn. Lyon 79: 1–22. https://doi.org/10.3406/linly.1936.14776

Larsson A. 2014. AliView: a fast and lightweight alignment viewer and editor for large datasets. Bioinformatics 30: 3276–3278.

Mata JL, Hughes KW, Petersen RH. 2004. Phylogenetic placement of *Marasmiellus juniperinus*. Mycoscience 45: 214–221. https://doi.org/10.1007/S10267-004-0170-3

Mata JL, Hughes KW, Petersen RH. 2007. An investigation of /omphalotaceae (*Fungi*: Euagarics) with emphasis on the genus *Gymnopus*. Sydowia 58(2): 191–289.

Matheny PB, Curtis JN, Hofstetter V, Aime MC, Moncalvo J-M, Gee Z-W, Yang Z-L & al. 2006. Major clades of *Agaricales*: a multilocus phylogenetic overview. Mycologia 98(6): 982–995. https://doi.org/10.1080/15572536.2006.11832627

Millspaugh CF 1913 The living flora of West Virginia. West Virginia Geol. Surv. 5(Pt.1): 1–389. https://doi.org/10.5962/bhl.title.56464

Moncalvo J-M, Lutzoni FM, Rehner SA, Johnson J, Vilgalys R. 2000. Phylogenetic relationships of agaric fungi based on nuclear large subunit ribosomal DNA sequences. Syst. Biol. 49: 278–305. https://doi.org/10.1093/sysbio/49.2.278

Moncalvo J-M, Vilgalys R, Redhead SA, Johnson JE, James TY, Aime MC & al. 2002. One hundred and seventeen clades of euagarics. Mol. Phyl. Evol. 23: 357–400. https://doi.org/10.1016/S1055-7903(02)00027-1

Murrill WO. 1915. *Marasmiellus* in *Agaricales*, *Agaricaceae*. North Amer. Fl. 9(4): 201–296.

MycoPortal. 2018. http://mycoportal.org (last searched 10/2019)

Nakasone K, Hibbett DS, Goranova G. 2009. *Neocampanella*, a new corticioid fungal genus, and a note on *Dendrothele bispora*. Botany 87: 875–882. https://doi.org/10.1139/B09-046

Oliveira JJS, Vargas-Isla R, Cabral TS, Rodrigues DP, Ishikawa NK. 2019. Progress on the phylogeny of the *Omphalotaceae*: *Gymnopus* s. str., *Marasmiellus* s. str., *Paragymnopus* gen. nov. and *Pusillomyces* gen. nov. Mycol. Prog. 18: 713–739. https://doi.org/10.1007/s11557-019-01483-5

Patouillard N. 1900. Essai taxonomique sur les familles et les genres des *Hymnomycetes*. Lons-le-Saunier. Reprint Ascher 1963. https://doi.org/10.5962/bhl.title.40287

Pegler DN, Young TWK. 1971. Basidiospore morphology in the *Agaricales*. Nova Hedwigia, Beih. 35: 210 p.

Petersen RH, Borovička J, Reboredo-Segovia A, Hughes KW. 2015. Transatlantic disjunction in fleshy fungi. II. The *Sparassis spathulata* - *S. brevipes* complex. Mycol. Prog. 14(30): [18 p]. https://doi.org/10.1007/s11557-015-1049-8

Petersen RH, Hughes KW. 2014. New North American species of *Gymnopus*. North Amer. Fungi 9(3): 1–22. https://doi.org/10.2509/naf2014.009.003

Petersen RH, Hughes KW. 2016. *Micromphale* sect. *Perforantia* (*Agaricales, Basidiomycetes*); Expansion and phylogenetic placement. MycoKeys 18: 1–122.

Petersen RH, Hughes KW. 2017a. Corrigenda for: "*Micromphale* sect. *Perforantia* (*Basidiomycetes*); Expansion and phylogenetic placement" published in MycoKeys. MycoKeys 19: 45–54.

Petersen RH, Hughes KW. 2017b. An investigation on *Mycetinis* (Euagarics, *Basidiomycota*). MycoKeys 24: 1-138.

Petersen RH, Hughes KW. 2020. Two new genera of gymnopoid/marasmioid euagarics. Mycotaxon 135: 1–95. https://doi.org/10.5248/135.1

Ridgway R 1912 Color standards and color nomenclature. Published Privately. 43 pp + 52 plates. https://doi.org/10.5962/bhl.title.62375

Saccardo PA 1887. Sylloge Fungorum omnium hucusque cognitorum. Vol. 5. Padua. 1144 pp.

Sandoval-Leiva PA, McDonald JW, Thorn RG. 2016. *Gymnoporella nothofagi*, a new genus and species of gymnopoid fungi (*Omphalotaceae*) from Chilean *Nothofagus* forest. Mycologia 108(4): 820-827. https://doi.org/10.3852/15-303

Singer R 1936. Das System der *Agaricales*. Ann. Mycol. 34: 287-378.

Singer R 1938. Notes sur quelque *Basidiomycetes*. Rev. Mycol. 2: 187-199.

Singer R 1948 ("1946"). New and interesting species of *Basidiomycetes*. Pap. Michigan Acad. Sci. 32: 103–150.

Singer R. 1950. Should D.P. Rogers' proposals for the regulation for fixing generic types be accepted as published in Mycologia 41: 219, 1949? Mycologia 42: 195–197. https://doi.org/10.2307/3755252

Singer R. 1962. The *Agaricales* in modern taxonomy. J. Cramer, Weinheim. 915 p. + 73 pls.

Singer R. 1973. A monograph of the neotropical species of *Marasmiellus*. Nova Hedwigia, Beih. 44: 1-340.

Thompson JD, Higgins DG, Gibson TJ. 1994. CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. Nucleic Acids Research 22: 4673–4680.

Turland NJ, Wiersema JH, Barrie FR, Greuter W, Hawksworth DL, Herendeen PS & al. 2018. International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Regn. Veget. 159. Glashütten: Koeltz Botanical Books. https://doi.org/10.12705/Code.2018

Wilson AW, Desjardin DE. 2005. Phylogenetic relationships in the gymnopoid and marasmioid fungi (*Basidiomycetes*, euagarics clade). Mycologia 98: 667–679. https://doi.org/10.3852/mycologia.97.3.667